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## Systematics of *Nanexila* Winterton & Irwin, gen. nov. (Diptera : Therevidae) from Australia

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### Abstract

*Nanexila* Winterton & Irwin, gen. nov. is described and figured from Australia. This genus of typically small, slender flies is divided into three species-groups following cladistic analysis. The previously unplaced *N. manni* (Hardy) comb. nov. is redescribed in the *Nanexila manni* species-group, along with four new species: *N. armeniacum*, *N. carminata*, *N. furcata* and *N. nana*. *Nanexila ruficornis* (Macquart) comb. nov. is redescribed in the *Nanexila palassa* species-group, along with ten new species: *N. argentiquadris*, *N. cylomelasma*, *N. danielsi*, *N. ligula*, *N. lignyos*, *N. livea*, *N. palassa*, *N. spilotis*, *N. variabilis*, and *N. vittata*. Four new species are described in the *Nanexila atricostalis* species-group: *N. atricostalis*, *N. aureilineata*, *N. intermedia*, and *N. paradoxa*. The twenty *Nanexila* species and five outgroup species were compared across 167 states in 71 characters. A cladistic analysis was conducted and the phylogenetic relationships of *Nanexila* discussed. *Nanexila* is endemic to Australia, with a largely southern distribution. Only *N. argentiquadris* and *N. cylomelasma* are known from northern Australia. Adult *Nanexila* have been collected between August and April, with the peak period of activity for most species during October and November. The duration of adult activity is related to latitude, with northern species active for longer periods than southern species.

### Introduction

The Therevidae are a cosmopolitan group of lower brachyceran Diptera found in a variety of habitats, with greatest diversity in semi-arid regions and woodland. The adults are nectar feeders of blossoms while the larvae are voracious, fossorial predators of other soil arthropods, often found in sandy, friable soils (Irwin and Lyneborg 1981*b*).

The Australian Therevidae have been poorly studied since the first Australian species (*Agapophytus australasiae*) was described by Guérin-Ménéville (1838). Kröber (1912*a–f*, 1913, 1928, 1929, 1932) produced numerous treatments on Australasian therevids in which 42 new species and most of the Australian genera were described. The Tasmanian Therevidae were revised by White (1914, 1915) including the enigmatic *Clesthentia aberrans* White. The first comprehensive familial revision of the Australian Therevidae was by Mann (1928, 1929, 1933), in which he gave preliminary keys to genera and species, and detailed descriptions of 28 new species. The Australian therevid fauna currently comprises 112 described species (Irwin and Lyneborg 1989; Colless and McAlpine 1991). There is a large amount of undescribed material in Australian and overseas collections awaiting formal description. This study is one of a series of treatments on the world Therevidae.

*Nanexila* Winterton & Irwin, gen. nov. are relatively small, slender flies with a maximum body length of eleven millimetres. They can be found in a variety of habitats, including grassland and open forest, and are commonly collected in semi-arid regions of southern Australia.

Hardy (1955) described *Anabarhynchus manni* Hardy from Katoomba, New South Wales, noting that this species differed from all other *Anabarhynchus* Macquart by the eyes of the male being contiguous. In a synoptic list of the Australasian and Oceanian Therevidae, Irwin and Lyneborg (1989) proposed removing *A. manni* from *Anabarhynchus*, but did not place the

species in an alternative genus. Macquart (1850) described *Anabarhynchus ruficornis* from 'Nelle Hollande' [probably a contraction of Nouvelle Hollande =Australia]. Mann (1928) did not examine any specimens of *A. ruficornis* but noted that the colouration is distinctive for the species. Irwin and Lyneborg (1989) supported the placement of *A. ruficornis* in *Anabarhynchus*. Lyneborg (1992) revised the New Zealand Therevidae, and found that *Anabarhynchus* includes a significant proportion of the therevid fauna in New Zealand and Australia.

In this study, *Nanexila* Winterton & Irwin, gen nov. is proposed to accommodate *A. manni* and *A. ruficornis*, and 18 new species are described. A phylogenetic analysis of *Nanexila* is presented, with the genus tentatively divided into three monophyletic species-groups. *Nanexila* is apparently endemic to Australia with a distinctly southern distribution, although two species are found in northern Australia.

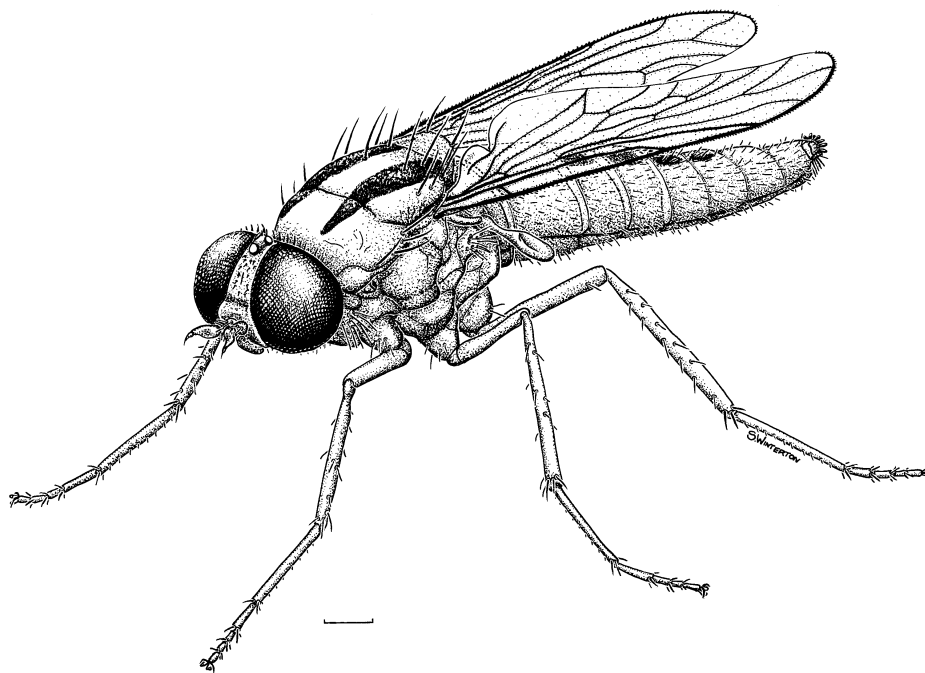


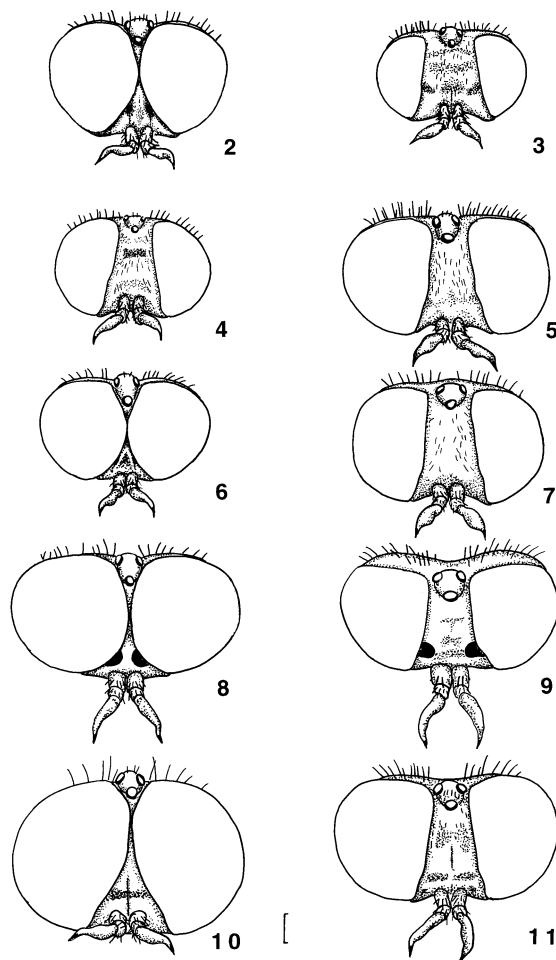
Fig. 1. Habitus, female: *Nanexila vittata* Winterton & Irwin, sp. nov., body length: 10 mm.

### Materials and methods

Genitalia were macerated to remove soft tissue in 10% KOH at 40–50°C for one hour, then rinsed and dissected in 80% ethanol. Female reproductive organs were stained with a saturated solution of Chlorazol Black in 40% ethanol. Preparations were then placed into glycerine gel and figures drawn using a camera lucida mounted on a Zeiss Stemi SV-6 stereo-microscope. Internal membranous structures of the female reproductive system were figured while still in ethanol as they collapse and distort when placed into glycerine or glycerine gel. Genitalia preparations are stored in glycerine and/or glycerine gel in a genitalia vial mounted on the pin underneath the specimen. Where possible, specimens examined are given a unique 'MEI' number (yellow label on specimen pin). These numbers represent entries in a therevid database and are quoted in parentheses in the list of material examined for future reference for specimen identification and location. New names are to be attributed to Winterton and Irwin.

### Terminology

There has been some inconsistency in the terminology used to describe therevid male genitalia (Irwin and Lyneborg 1981*a,b*; Nagatomi and Lyneborg 1987*a,b*; Yeates 1992, 1994; Lyneborg 1992; Sinclair 1992; Ovtshinnikova and Yeates 1998) (Table 1). This confusion centres around the use of paramere and parameral apodeme by Irwin and Lyneborg (1981*a*) to describe the structures termed inner gonocoxal process and gonocoxal apodeme (respectively) in this study (Fig. 34). Amongst the lower Brachycera, it is generally accepted that the parameres have become fused medially to enclose the aedeagus in a conical-



**Figs 2–11.** Head, anterodorsal view: 2, *Nanexila carminata* Winterton & Irwin, sp. nov. (♂); 3, *N. carminata* Winterton & Irwin, sp. nov. (♀); 4, *N. nana* Winterton & Irwin, sp. nov. (♀); 5, *N. manni* Winterton & Irwin, sp. nov. (♀); 6, *N. variabilis* Winterton & Irwin, sp. nov. (♂); 7, *N. variabilis* Winterton & Irwin, sp. nov. (♀); 8, *N. cylomelasma* Winterton & Irwin, sp. nov. (♂); 9, *N. cylomelasma* Winterton & Irwin, sp. nov. (♀); 10, *N. livea* Winterton & Irwin, sp. nov. (♂); 11, *N. livea* Winterton & Irwin, sp. nov. (♀). Scale line: 0.2 mm.

shaped sheath (the aedeagal or parameral sheath) (McAlpine 1981; Wood 1991; Sinclair *et al.* 1994). The male genital musculature supports this idea. In the Therevidae and other Asiloidea the paramere is connected to the ejaculatory apodeme by muscle M31 (Ovtshinnikova 1989; fig. 203). However, the inner gonocoxal process is connected to the gonocoxite by muscle M38 (Ovtshinnikova and Yeates 1998), indicating that it is gonocoxal in origin and not a fusion of the paramere to the gonocoxite.

The terminology for the male genitalia used in this study and that used by previous therevid workers are summarised in Table 1. (See Yeates (1994) for a comparison of terminology across the Asiloidea). To bring therevid terminology into agreement with that across the lower Brachycera the term 'inner gonocoxal process' is proposed to replace 'paramere' of Irwin and Lyneborg (1981*a,b*) and 'outer style' of Lyneborg (1992), while 'gonocoxal apodeme' is proposed to replace 'parameral apodeme' of Irwin and Lyneborg (1981*a,b*) and Nagatomi and Lyneborg (1987*a,b*).

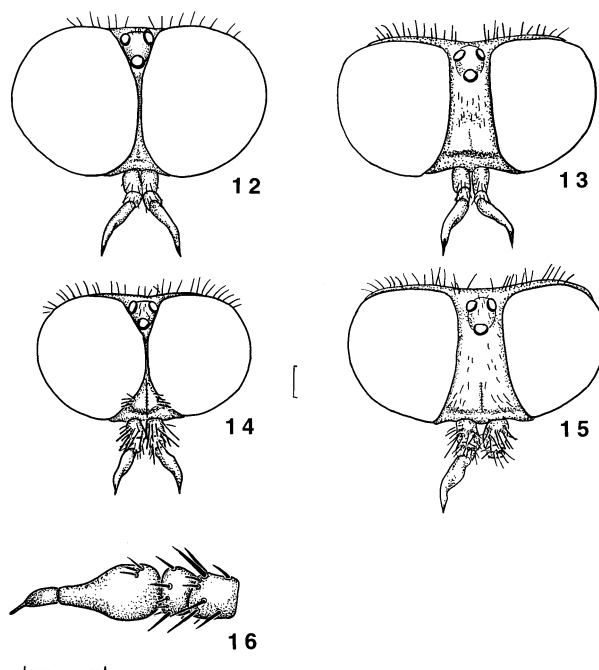
Terminology of the body vestiture follows Irwin and Lyneborg (1981*a*) and Yeates (1988), but the inconsistency of vestiture terminology amongst dipterists warrants that the terminology used here is clearly defined. Hairs or pile are long thin macrotrichia with well-developed basal sockets. Setae (including bristles) are thick, tapering macrotrichia of varying length with longitudinal fluting, also with well-developed basal

sockets. Scutal bristles are large setae used in scutal chaetotaxy. Pruinescence is composed of microtrichia which give a metallic, 'shagreen' appearance and is commonly found on the head and thorax, but less so on the abdomen in significant densities. Each microtrichium is recumbent, often with a longitudinal furrow to facilitate acute reflexion, and may be apically spatulate (Fig. 17a). The Latin term 'velutium' (velutinous pruinescence) is used here to describe pruinescence that is a metallic, often blue-silver coloured covering of short, acuminate microtrichia (Fig. 17b). The result is a reflective, velvet-like appearance. The appressed, unidirectional orientation and reflective nature of these microtrichia make them highly visible when viewed side on, but dull grey when viewed end on. Velutium is often present on the abdomen of males of some species (e.g. *N. ruficornis* (Macquart) and *N. palassa* Winterton & Irwin, sp. nov.) and occasionally of females. Irwin and Lyneborg (1981a) refer to this vestiture as pollen. 'Matt' pruinescence is a type of pruinescence which is dull in appearance and is not reflective when viewed from any direction. This pruinescence is typically matt black in colour. The term velvet has been used by Cole (1923, 1960) and Irwin and Lyneborg (1981a) to describe matt pruinescence in Neartic Therevidae, but is not used here to avoid confusion with velutium.

#### Abbreviations used

(i) The following abbreviations have been used for collections from which specimens were examined:

AM	Australian Museum, Sydney
ANIC	Australian National Insect Collection, CSIRO Entomology, Canberra
CAS	Californian Academy of Sciences, San Francisco
CNC	Canadian National Collection, Ottawa
GDCB	Greg Daniels Collection, University of Queensland, Brisbane
IRWC	Mike Irwin Collection, University of Illinois, Champaign
MNHN	Muséum National d'Histoire Naturelle, Paris
QDPI	Queensland Department of Primary Industries, Brisbane
QM	Queensland Museum, Brisbane
SAM	South Australian Museum, Adelaide
TAMU	Texas A&M University, College Station
UQIC	University of Queensland Insect Collection, Brisbane



**Figs 12–15.** Head, anterodorsal view: 12, *Nanexila vittata* Winterton & Irwin, sp. nov. (♂); 13, *N. vittata* Winterton & Irwin, sp. nov. (♀); 14, *N. atricostalis* Winterton & Irwin, sp. nov. (♂); 15, *N. atricostalis* Winterton & Irwin, sp. nov. (♀). **Fig. 16.** *N. danielsi* Winterton & Irwin, sp. nov.: left antenna, left lateral view.

WADA Western Australian Department of Agriculture, Perth  
 WAM Western Australian Museum, Perth

(ii) The following abbreviations have been used for morphological terms and scutal chaetotaxy:

Scutal chaetotaxy:

dc dorsocentral setae  
 np notopleural setae  
 pa post-alar setae  
 sa supra-alar setae  
 sc scutellar setae

Genitalic terms:

ac accessory gland  
 A1 A1 setae (= acanthophorites)  
 A2 A2 setae  
 bea base of ejaculatory apodeme  
 ce cercus  
 d distiphallus  
 da dorsal apodeme of parameral sheath  
 ea ejaculatory apodeme  
 f furca  
 ga gonocoxal apodeme  
 gc gonocoxite  
 gs gonostylus  
 hy hypandrium  
 igp inner gonocoxal process  
 lep lateral ejaculatory process  
 ogp outer gonocoxal process  
 ses subepandrial sclerite  
 sp spermatheca  
 spd spermathecal duct  
 sps spermathecal sac  
 ssd spermathecal sac duct  
 s8 sternite 8  
 t8 tergite 8  
 va ventral apodeme of parameral sheath  
 vl ventral lobe

#### *Male genitalic dimension ratios*

The ratio of the epandrium width at the midpoint to the epandrium length along the midline was determined (Fig. 39). Similarly, the ratio of the width of the base of the ejaculatory apodeme to the total length of the ejaculatory apodeme was also determined (Figs 41, 42).

#### **Taxonomy**

Based on genitalic features, Irwin and Lyneborg (1981a) divided the Nearctic Therevidae into two subfamilies: Therevinae and Phycinae. The Australasian Therevidae do not conform to this classification and most probably represent a separate, undescribed subfamily. This group contains the speciose genus *Agapophytus* Guérin-Méneville and we designate it here as the '*Agapophytus* group'. The subfamily Phycinae is absent from Australia while *Anabarhynchus* belongs within the Therevinae. The *Agapophytus* group can be distinguished from *Anabarhynchus* by the presence of three spermathecae and the femoral vestiture being erect, and uniform in size and length.

The following combination of synapomorphies enable identification of *Nanexila* within the Australian Therevidae: (a) cell  $m_3$  open, (b) one pair of scutellar setae, (c) three or more pairs of dorsocentral setae, (d) flagellum conical, tapering gradually, (e) scape much shorter than flagellum, (f) antennal tubercle absent, (g) outer gonocoxal process present, (h) matt pruinose patches on fore and hind femora absent (possibly the plesiomorphic condition), (i) single seta present on hind femur, (j) dorsal apodeme of aedeagal sheath enlarged, (k) ventral apodeme of aedeagal sheath reduced.

**Table 1. Comparison of male genitalia terminology used in this study with that used by previous therevid workers**

Terms used here	pre- Irwin and Lyneborg (1981 <i>a</i> )	Irwin and Lyneborg (1981 <i>a</i> )	Irwin and Lyneborg (1981 <i>b</i> )	Nagatomi and Lyneborg (1987 <i>a</i> )	Nagatomi and Lyneborg (1987 <i>b</i> )	Lyneborg (1992)	Yeates (1992, 1994)	Sinclair <i>et al.</i> (1994)	Ovtshinnikova and Yeates (1998)
ventral lobe	ventral lobe	ventral lobe	ventromedial lobe/ aedeagal guide	ventral lobe	ventral lobe	ventral lobe	–	–	ventral lobe
gonostylus	gonostylus	gonostylus	gonostylus	gonostylus	gonostylus	inner style/ gonostyle	gonostylus	gonostylus	gonostylus
inner gonocoxal process	parameral process	paramere (=dorsal gonocoxal process)	paramere	parameral process	parameral process	outer style	–	–	parameral process
outer gonocoxal process	outer gonocoxal process	‘gonocoxal lobe’	gonocoxal process	–	knoblike process	‘posterior extension’ of gonocoxite	posterior process of gonocoxa	–	outer gonocoxal process
ventral gonocoxal process	ventral – gonocoxal process	–	–	–		‘posteromedial – extension’ of gonocoxite	–	–	–
gonocoxite	gonocoxite	gonocoxite	gonocoxite	gonocoxite	gonocoxite	gonocoxite	gonocoxa	gonocoxite	gonocoxite
gonocoxal apodeme	dorsal gonocoxal process	parameral apodeme	parameral apodeme	parameral apodeme	parameral apodeme	gonocoxal apodeme	gonocoxal apodeme	gonocoxal apodeme	gonocoxal apodeme





Genus *Nanexila* Winterton & Irwin, gen. nov.

Type species: *Anabarhynchus manni* Hardy, 1955.

*Description*

Body length (range): 4–8 mm (male); 5–11 mm (female).

*Head* (Figs 1–15). Head shape round, hypognathous; eyes representing a large proportion of head area; frons colour variable, pruinose, female with short, sparsely distributed setae, setae present or absent in male; eye facets usually larger in upper section than those in lower; ocellar tubercle with several small dark setae; occiput and gena brown or grey pruinose; postocular ridge in male with single (rarely two) row of black setae, two rows present in female (rarely one); palps small, pale; antennal tubercle absent; antenna pale, pruinose; scape and pedicel cylindrical, scape slightly longer than pedicel but shorter than flagellum, dark setae present, scape with some distal setae enlarged, number variable; flagellum conical, tapering to a point (Fig. 16), flattened laterally, often with two to four small setae at base of first segment, colouration usually orange, style dark, terminal.

*Thorax* (Figs 22–29). Considerable intra- and inter-specific variation in scutum colouration and markings, ground colour pale yellow-grey to brown pruinose; markings, if present, usually composed of median stripe(s) and/or broken lines or spots laterally; often with small dark setae sparsely covering scutum, all thoracic macrosetae (bristles) dark (exceptions rare), notopleural and supra-alar setal number variable interspecifically, dorsocentral setae number variable intra- and interspecifically; setae on pteropleural callus usually pale but may have some or all dark, admixed; hind coxa with one or two lateral setae, number variable intra- and interspecifically; fore and mid-legs pale yellow, hind femur sometimes darkened, single lateroventrally directed seta positioned distally (Fig. 1); terminal tarsal segments on all legs usually darkened; wing hyaline, rarely infuscate; cell  $m_3$  open, vein  $R_1$  glabrous. Scutal chaetotaxy (range): np 3–4; sa 1–2; pa 1; dc 3–7; sc 1.

*Abdomen* (Figs 17b,d, 22–29). Abdomen elongate, pruinescence sometimes present; colour commonly black or yellow; species with yellow abdomens sometimes with dark medial spots, occurrence sometimes sexually dimorphic; males with dark abdomens often with silver velutum laterally and ventrally, intensity highly variable, female abdomen rarely with velutum (except *N. atricostalis* species-group); male with long pale hairs laterally on segments 1–7, absent in female; females of *N. palassa* species-group with modified patch of setae located posteromedially on tergite 2 (Fig. 17c, d), shape and arrangement of setae variable; intersegmental membranes usually pale.

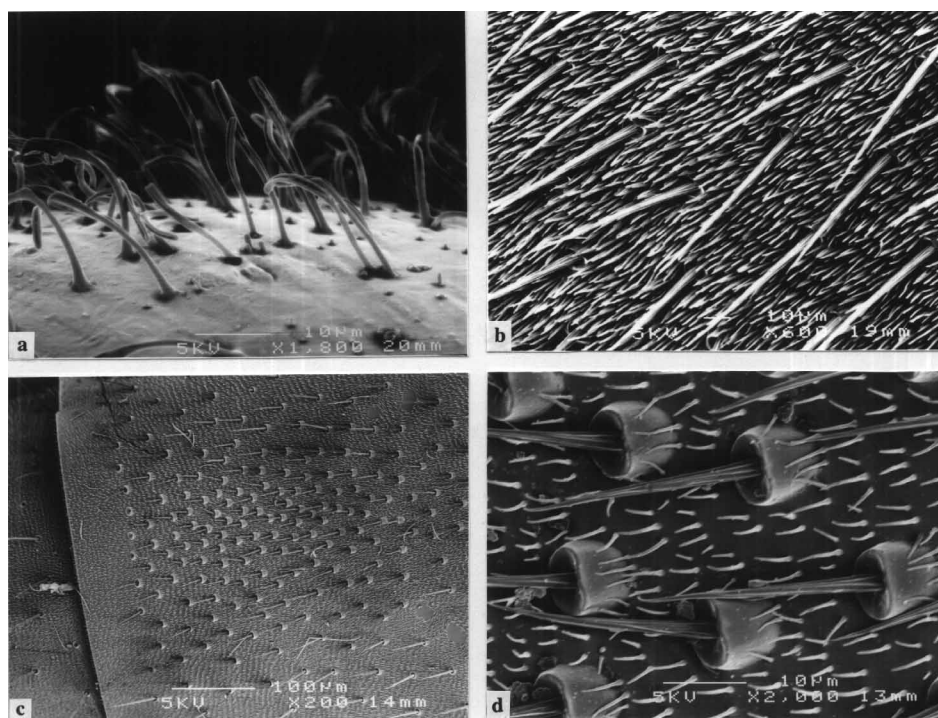
*Male genitalia*. Epandrium quadrate to elongate, posterolateral processes absent (e.g. *N. variabilis* Winterton & Irwin, sp. nov.) to greatly enlarged (e.g. *N. ruficornis*), enlarged setae present or absent posterolaterally; tergite 8 narrow to broad, posterior margin often medially emarginate; gonocoxites separate or fused medially; hypandrium separate or fused with gonocoxites; gonocoxal apodemes reduced, rarely enlarged; ventral lobe reduced or enlarged, apical setae present or absent; gonostylus simple, furcate in *N. furcata* Winterton & Irwin, sp. nov.; usually with medial and ventral setae, sometimes sclerotised apically; inner gonocoxal process narrow or spatulate, apical setae often present; outer gonocoxal process present, enlarged setae apically; enlarged setae arranged in series ventrally in some species; distiphallus narrow, straight, or curved; dorsal apodeme triangular or forked, enlarged, usually secondarily forked distally; ventral apodemes forked, sometimes only apically; size of base of ejaculatory apodeme variable relative to rest of ejaculatory apodeme and aedeagus, lateral aedeagal process present.

*Female genitalia*. Furca well sclerotised, open or closed anteriorly; sternite 10 narrowed posteriorly, posterior margin cleft medially; A1 setae number 4–8; A2 setae number 6–9; three spermathecae; spermathecal ducts entering into common spermathecal sac duct(s) in one of three different arrangements: (a) basally, with all three spermathecal ducts entering into the common spermathecal sac duct (e.g. Figs 61, 79, 107), (b) paired, with a spermathecal duct entering each individual spermathecal sac duct before they unite to form the common spermathecal sac duct (Figs 125, 171, 174, 180), or (c) alternate, with a spermathecal duct entering the common spermathecal sac duct alternate to each spermathecal sac duct (Fig. 177); spermathecal sac

arrangement of two basic types: simple (e.g. Figs 61, 110) or trilobate (e.g. Fig. 79, 171, 177), trilobate sacs varying in relative size of each sac; sacs elongate or globose; accessory glands asymmetrical (e.g. Fig. 110) or symmetrical (e.g. Fig. 98), rarely modified (Fig. 70).

### Comments

Species of *Nanexila* exhibit different levels of sexual dimorphism. As found in most other Diptera the frons is narrower in the male (e.g. Fig. 2) than the female (e.g. Fig. 3). In species such as *N. atricostalis* Winterton & Irwin, sp. nov. and *N. manni*, the female is slightly larger than the male. Dark medial spots on the abdominal tergites are found only in the female in *N. argentiquadris* Winterton & Irwin, sp. nov. and *N. vittata* Winterton & Irwin, sp. nov., but in both sexes of *N. spilotis* Winterton & Irwin, sp. nov. and *N. cylomelasma* Winterton & Irwin, sp. nov. The commonest form of sexual dimorphism in *Nanexila* species is in the size and arrangement of hairs and setae. Short frontal setae are present only in the female of many species. In all species abdominal segments 1–4 or 1–5 of the male have long, pale hairs laterally. In the female these hairs are replaced by sparsely distributed short, black setae. Females of the *N. palassa* species-group also have a patch of short modified setae posteromedially on abdominal tergite 2 (Fig. 17c,d). The degree of modification varies with species, with the greatest development in *N. vittata*. Similar, more specialised setal patches are found in certain other therevid genera (e.g. *Neodialineura* Mann, *Bonjeania* Irwin & Lyneborg) and in the Scenopinidae (Yeates 1992), the function of this setal patch is unknown, but appears to be sensory. The setal patch of *Neodialineura* and *Bonjeania* differs slightly in shape and setal structure, and is found in both the male and female (Winterton unpublished data), while in those species of *Nanexila* which have the setal patch, it is found only in the female.



**Fig. 17a–d.** Scanning electron micrographs of Therevidae vestiture: (a) *Neodialineura striatithorax* Mann (♂), pruinence on antennal tubercle (scale line: 10 µm); (b) *Agapophytus aterrimus* Mann (♂), abdominal setae admixed with dense velutum (reflective, silver pruinence) (scale line: 10 µm); (c) *Nanexila vittata* Winterton & Irwin, sp. nov. (♀), abdominal tergite 2, dorsal view showing posteromedial patch of modified setae (scale line: 100 µm); (d) close up of modified setae admixed with sparse microtrichia (pruinence) (scale line: 10 µm).

The female reproductive system of Australasian Therevidae has a large sac-like structure associated with the spermathecal ducts. This sac, termed here the spermathecal sac, is variable in shape and size, representing over 75% of the abdominal volume in some species. The sac arrangement may be simple or trilobed, with trilobed sacs varying in arrangement of the spermathecal sac ducts to the spermathecal ducts (i.e. basal, paired or alternate). The function of the spermathecal sac is unknown, but ongoing histological studies by the authors indicate that it may be used as a receptacle for male accessory gland secretions during copulation (e.g. nuptial gift).

The pupa is known for *N. vittata* and *N. manni*. English (1950) found that the presence or absence of the alar spine above the wing sheath varied between genera examined. She found that the spine is present in *Anabarhynchus* and *Platycarenum* Kröber, and absent in *Agapophytus* Guérin-Ménéville, *Ectinorhynchus* Macquart, and *Acraspisa* Kröber. The alar spine is also absent *Nanexila*. Lyneborg (1992) proposed that this character may be important phylogenetically and that the presence of the alar spine is probably the apomorphic state. The presence of the alar spine in several Holarctic therevine genera (e.g. *Thereva* Latrielle, *Dialineura* Rondani, *Acrosathe* Irwin & Lyneborg) (Lyneborg 1992), and the placement of *Anabarhynchus* and *Platycarenum* in the Therevinae suggest that it may be apomorphic for that subfamily.

Several damaged specimens examined during this study represent distinct species that fall within the limits of *Nanexila*; they are not described here due to their poor condition.

#### Etymology

Latin *nana*: a dwarf; *exilis*: thin, slender; referring to the small size and slender form of the species in this genus. Gender is feminine.

#### Key to species of *Nanexila*

The following key to species-groups and species is based largely on external morphology where possible and supplemented with genitalic characters. Many species are distinct and key solely on external characters, but genitalic examination will confirm identification. Species such as *N. variabilis*, *N. manni* and *N. danielsi* Winterton & Irwin, sp. nov. display considerable variation in external morphology, while *N. danielsi*, *N. ligula* Winterton & Irwin, sp. nov. and female *N. palassa* cannot be reliably separated solely on external characters. The likely collection of undescribed species also warrants close reference to species descriptions and genitalia figures. The male genitalia and female spermathecal sac arrangement and morphology are characteristic at species level, thus figures of male and female genitalia including female sac arrangement are provided for each species.

1. Epandrium without enlarged setae (e.g. Fig. 30); female abdominal tergite 2 without patch of modified setae ..... 2  
     Epandrium with enlarged setae laterally or posterolaterally (e.g. Figs 101, 119, 147); female abdominal tergite 2 with patch of modified setae posteromedially (Fig. 17c,d) .....  
     ..... *Nanexila palassa* species-group 3
2. Male frons with setae; epandrium broad, without posterolateral processes (Fig. 165); ventral lobe not enlarged (Fig. 169); female abdomen, *or* at least margins of tergites with velutum; spermathecal sac arrangement trilobate, never simple; alternate or paired spermathecal duct arrangement (Figs 171, 174, 177, 180) ..... *Nanexila atricostalis* species-group 13  
     Male frons without setae; epandrium elongate, with posterolateral processes (Fig. 56); ventral lobe enlarged, more than half the length of gonostylus (Fig. 43); female abdomen without velutum; spermathecal sac simple (e.g. Fig. 61), rarely trilobate (Fig. 53); basal spermathecal duct arrangement (e.g. Fig. 61) ..... *Nanexila manni* species-group 16
3. Scutum pale yellow or grey, basal socket of all setae dark (Fig. 26); base of ejaculatory apodeme greatly enlarged (e.g. Figs 84, 103); gonocoxites with groups of enlarged setae arranged in series (e.g. Fig. 106, 118); female spermathecal sac always simple, without lateral branches or lobes (e.g. Figs 88, 110) ..... 4  
     Scutum variously coloured, at most basal sockets of macrosetae darkened slightly; base of ejaculatory apodeme not greatly enlarged (e.g. Fig. 75, 157); gonocoxites without enlarged setae *or*, if present, then restricted to the outer gonocoxal process and never arranged in series (Fig. 151); spermathecal sac arrangement variable, simple or multi-lobed (e.g. Figs 79, 98, 125) ..... 9

4. Wing venation dark, veins surrounded with dark infuscation (Fig. 18); hind femur dark; female spermathecal sac duct extremely long, thin and convoluted (Fig. 110); male unknown ..... *N. lignyos* Winterton & Irwin, sp. nov.  
Wing venation light or dark, veins not surrounded with dark infuscation, hind femur pale; female spermathecal sac duct relatively short and thick, straight or slightly convoluted (e.g. Figs 88, 107) ..... 5
5. Male abdomen covered with silver velutum; anterior apodemes of gonocoxites small, less than one third of total length of gonocoxite; ventral lobe of gonocoxites without setae; female spermathecal sac elongate, cylindrical; duct short, relatively straight (Figs 88, 135) ..... 6  
Male abdomen without silver velutum; anterior apodemes of gonocoxites large, representing approximately one third to one half the total length of gonocoxite; setae on ventral lobe of gonocoxites (Figs 117, 142); female spermathecal sac ovate; duct long, convoluted (Figs 107, 144) ..... 7
6. Abdominal tergites with dark medial markings; epandrium with posterolateral corners elongate, projecting posteroventrally and encompassing cerci (Fig. 82); female postocular ridge with two rows of setae; spermathecal sac quadrangular shaped (Fig. 88) ..... *N. ruficornis* (Macquart)  
Abdominal tergites unmarked; epandrium without posterolateral corners projecting (Fig. 129); female postocular ridge with single row of setae; spermathecal sac rounded, not quadrate (Fig. 135) ..... *N. palassa* Winterton & Irwin, sp. nov.
7. Abdominal tergites with dark median spots (Fig. 26); scutum and scutellum concolourous, either tan or grey ..... *N. spilotis* Winterton & Irwin, sp. nov.  
Abdominal tergites without dark median spots; scutum grey and scutellum yellow-tan coloured ..... 8
8. Epandrium with enlarged setae concentrated posterolaterally (Fig. 113); distiphallus short (Fig. 116); posterior end of subepandrial sclerite ladle shaped (Fig. 118); female unknown ..... *N. ligula* Winterton & Irwin, sp. nov.  
Epandrium with enlarged setae distributed along lateral margin (Fig. 101); distiphallus long (Fig. 104); posterior edge of subepandrial sclerite simple, not ladle shaped ..... *N. danielsi* Winterton & Irwin, sp. nov.
9. Scutum with quadrate patch (either silver pruinose or dark brown) located between and bordered by dorsocentral setae (Figs 23, 24, 27); male aedeagus with arms of ventral apodeme broad, paddle shaped (Figs 75, 94, 157) ..... 10  
Scutum without quadrate patch; male aedeagus with arms of ventral apodeme thin, not paddle shaped (Figs 121, 148) ..... 12
10. Frons with a single black spot under each eye (Figs 8, 9), abdominal tergite markings variable but found in male and female (Fig. 24); female spermathecal sac simple, elongate (Fig. 98) ..... *N. cyclomelasma* Winterton & Irwin, sp. nov.  
Frons without black spots beneath the eye, abdominal tergite markings only found in female (Figs 23, 27), male abdomen bare; female spermathecal sac trilobate, single median sac with two smaller sacs laterally (Figs 79, 161) ..... 11
11. Scutum with two dark brown longitudinal stripes; pruinose scutal quadrate without pruinose arms projecting anteriorly (Fig. 27); wing venation dark; female with dark transverse stripe across frons (Fig. 13); male distiphallus straight (Fig. 158) ..... *N. vittata* Winterton & Irwin, sp. nov.  
Scutum without brown longitudinal stripes; pruinose scutal quadrate often with pruinose arms projecting anteriorly (Fig. 23); wing venation pale; female with frons bare; male distiphallus recurved dorsally (Fig. 76) ..... *N. argentiquadris* Winterton & Irwin, sp. nov.
12. Abdomen colour yellow, tergites often darkened medially; scutum brown or grey, unpatterned; frons without transverse pruinose stripe; male epandrium broad, quadrangular (Fig. 147); gonocoxites without posteroventral process between ventral lobe and posterior projection of gonocoxite (Fig. 151); aedeagus with distiphallus short, straight; ventral apodeme secondarily forked (Figs 148, 149); female spermathecal sac arrangement simple (Fig. 152) ..... *N. variabilis* Winterton & Irwin, sp. nov.  
Thorax and abdomen patterned as in Fig. 25, scutum blue grey pruinose with brown pattern, frons of both sexes with transverse, pruinose stripe (Figs 10, 11); male epandrium elongate (Fig. 119); gonocoxites with posteroventral process between ventral lobe and posterior projection of gonocoxite (Fig. 119); distiphallus long, recurved ventrally; ventral apodeme not secondarily forked (Figs 121, 122); female spermathecal sac arrangement trilobate, spermathecal sacs elongate (Fig. 125) ..... *N. livea* Winterton & Irwin, sp. nov.
13. Wing hyaline or at most with uniform pale infuscation ..... 14  
Costal area of wing with dark infuscation (Figs 20, 21) ..... 15

14. Wing with pale infuscation; setae on postocular ridge dark; setae on pteropleural callus mostly pale; scutum with four notopleural setae and two supra-alar setae; lobes of spermathecal sac with apical constriction to form a small, distal sac (Fig. 180); male unknown ..... *N. paradoxa* Winterton & Irwin, sp. nov.  
 Wing hyaline; postocular ridge with anterior row of setae dark, posterior row pale; scutum with three notopleural setae and one supra-alar setae; setae on pteropleural callus dark; lobes of spermathecal sac without apical constriction (Fig. 177); male unknown ..... *N. intermedia* Winterton & Irwin, sp. nov.
15. Occiput grey pruinose; scutum silver-green pruinose; scutum with three notopleural setae and one supra-alar seta; abdominal tergites with at most only faint silver velutum, patterned as in Fig. 28; spermathecal sacs of female approximately the same size as spermathecae ..... *N. atricostalis* Winterton & Irwin, sp. nov.  
 Occiput gold pruinose; scutum with gold pruinose stripe, brown laterally; scutum with four notopleural setae and two supra-alar setae; abdominal tergites 2–5 with silver velutum laterally, patterned as in Fig. 29; spermathecal sacs of female much larger than spermathecae; male unknown ..... *N. aureilineata* Winterton & Irwin, sp. nov.
16. Abdomen colour orange, sometimes tergites with medial spots or markings; male aedeagus with dorsal apodeme broad, triangular (Figs 32, 51) ..... 17  
 Abdomen colour mostly dark, lateral margins of tergites sometimes pale, markings or spots absent; male aedeagus with dorsal apodeme narrow, forked, 'T' shaped (Figs 41, 57, 66) ..... 18
17. Coxal setae black; two rows of setae on postocular ridge of male; thorax with two thin longitudinal stripes; male hypandrium fused with gonocoxites (Fig. 34); gonostylus simple (Fig. 35); female spermathecal sac simple (Fig. 36) ..... *N. armeniacum* Winterton & Irwin, sp. nov.  
 Coxal setae pale brown; single row of setae on postocular ridge of male; thorax sometimes with two faint longitudinal stripes; male hypandrium separate from gonocoxites (Fig. 51); gonostylus forked (Fig. 52); female spermathecal sac trilobate, single median sac with two smaller sacs laterally (Fig. 53) ..... *N. furcata* Winterton & Irwin, sp. nov.
18. Abdominal tergites 2–4 pale laterally; frons of female wrinkled with tentorial pits darkened (Fig. 3); male with a set of 'comb'-like setae on ventral edge of gonostylus (Fig. 44) ..... *N. carminata* Winterton & Irwin, sp. nov.  
 Abdominal tergites wholly dark, frons of female only slightly wrinkled, tentorial pits pale or only slightly darkened; male gonostylus without 'comb'-like setae ventrally (Figs 60, 69) ..... 19
19. Abdominal intersegmental membranes vivid white; males with silver pruinescence on abdomen; thorax silver-grey pruinose with dark brown patterning (Fig. 22); female spermathecal sac elongate, cylindrical, accessory glands separate (Fig. 61); male with posterolateral margin of epandrium projected to fine point (Fig. 56) ..... *N. manni* (Hardy)  
 Abdominal intersegmental membranes dull white; male abdomen without silver pruinescence; thorax colour uniform grey or brown, rarely with faint markings; female spermathecal sac balloon shaped, accessory glands intimate, interdigitate (Fig. 70); male with posterolateral margin of epandrium thickened, rounded, not projecting posteriorly (Fig. 64) ..... *N. nana* Winterton & Irwin, sp. nov.

### *Nanexila manni* species-group

This species-group (clade 10; Figs 184, 185) contains typically small-sized species, including the type species *N. manni*, and is differentiated by the following combination of characters: enlarged ventral lobe, elongate epandrium; unmodified setae on the epandrium and gonocoxites; narrow inner gonocoxal processes; absence of modified setae on female abdominal tergite 2.

### *Nanexila armeniacum* Winterton & Irwin, sp. nov.

(Figs 30–38, 73)

#### *Material examined*

*Holotype*. ♂, Western Australia: Albany, 17.xi.1958, E.F. Riek (MEI#028737) (ANIC). Condition: good.

*Paratypes*. **South Australia**: ♀, Pemberton, 24.xi.1978, S.J. Curry, Crowea First trap (MEI#028739) (ANIC); ♀, Seal Bay, Kangaroo Is., 5.xii.1977, D.K. McAlpine & M.A. Schneider (MEI#029208) (AM);

**Western Australia:** 2 ♀, Porongurup Natl Pk, Yate Flats, 9.xi.1987, M.E. Irwin & E.I. Schlinger, malaise trap (MEI#028735, 28738) (ANIC); ♀, Walyunga Natl Pk, 10–16.xi.1987, M.E. Irwin & E.I. Schlinger, malaise trap (MEI#028736) (ANIC).

### Diagnosis

Body colouration orange; postocular ridge of male with two rows of setae; coxal setae dark; dorsal apodeme of aedeagus triangular; spermathecal sac simple.

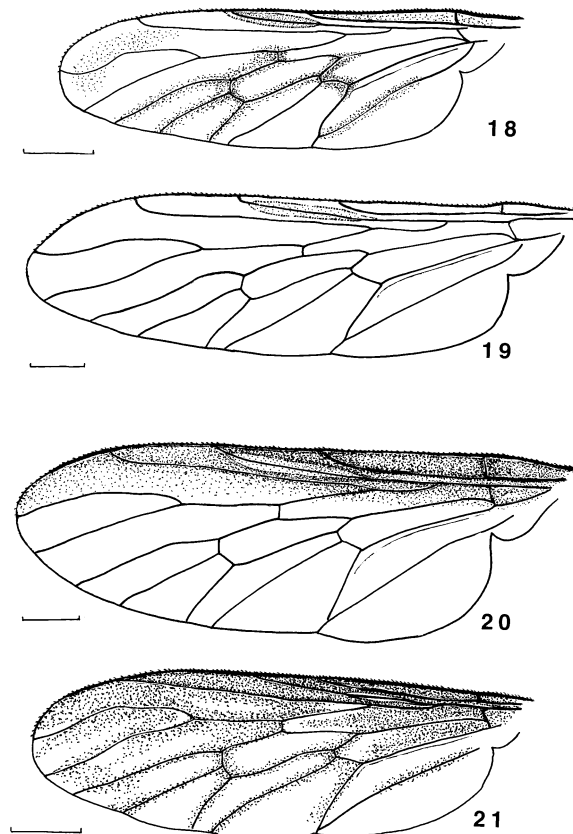
### Description

#### Male

Body length: 5 mm.

**Head.** Frons narrower than width of ocellar tubercle, golden pruinose above level of antennal bases; eyes proximate, not contiguous, eye facets uniform size throughout; ocellar tubercle ground colour black, golden pruinose; gena silver pruinose with short dark setae; palp short, pale orange, distal segment slightly bulbous; labellum dark orange; occiput silver pruinose; postocular ridge with two rows of black setae; scape and pedicel golden pruinose with short black setae; flagellum orange, darkened distally, two short setae located dorsally on basal segment.

**Thorax.** Integumental colour dark orange with gold pruinescence; sometimes with two thin longitudinal stripes along line of dorsocentral setae; legs pale; coxal setae dark; hind coxa with

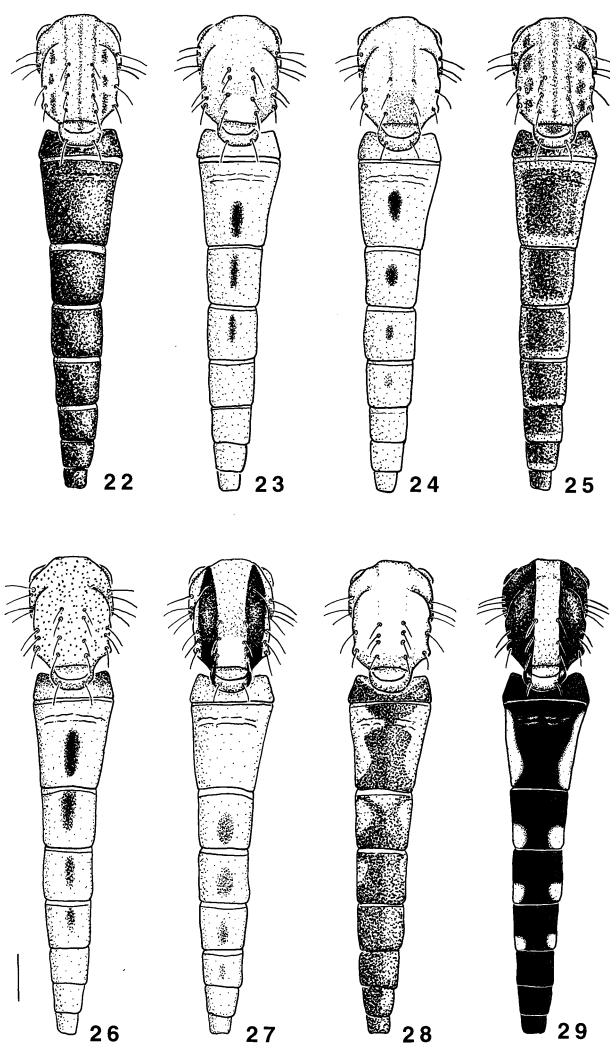


**Figs 18–21.** Wing, left: 18, *Nanexila lignyos* Winterton & Irwin, sp. nov.; 19, *N. vittata* Winterton & Irwin, sp. nov.; 20, *N. atricostalis* Winterton & Irwin, sp. nov.; 21, *N. aureilineata* Winterton & Irwin, sp. nov. Scale lines: 1.0 mm.

single lateral seta; wing hyaline, venation pale; haltere pale. Scutal chaetotaxy: np 3; sa 1; dc 4–5; pa 1; sc 1.

**Abdomen.** Colour pale yellow-orange; intersegmental membranes white; tergites 4–7 darkened slightly; segment 1 with long pale hairs; rest of abdominal segments with dark slightly shorter setae, very short towards middle of tergites.

**Genitalia (Figs 30–35).** Epandrium with rounded processes posteriorly, width to length ratio: 0.94; tergite 8 slightly constricted medially; gonocoxites separate; hypandrium not discernible, i.e. fused with gonocoxites, or absent; gonostylus with ventral and medially directed setae, thickened and slightly hooked apically; inner gonocoxal process slender, small setae apically; aedeagal complex relatively small; distiphallus slightly recurved dorsally; ventral apodeme forked; dorsal apodeme triangulate, enlarged; *bea* width to length: 0.35.



**Figs 22–29.** Thorax and abdomen, dorsal: 22, *Nanexila manni* Winterton & Irwin, sp. nov. (♀); 23, *N. argentiquadris* Winterton & Irwin, sp. nov. (♀); 24, *N. cylomelasma* Winterton & Irwin, sp. nov. (♂); 25, *N. livea* Winterton & Irwin, sp. nov. (♂); 26, *N. spilotis* Winterton & Irwin, sp. nov. (♀); 27, *N. vittata* Winterton & Irwin, sp. nov. (♀); 28, *N. atricostalis* Winterton & Irwin, sp. nov. (♂); 29, *N. aureilineata* Winterton & Irwin, sp. nov. (♀). Scale line: 1 mm.

*Female*

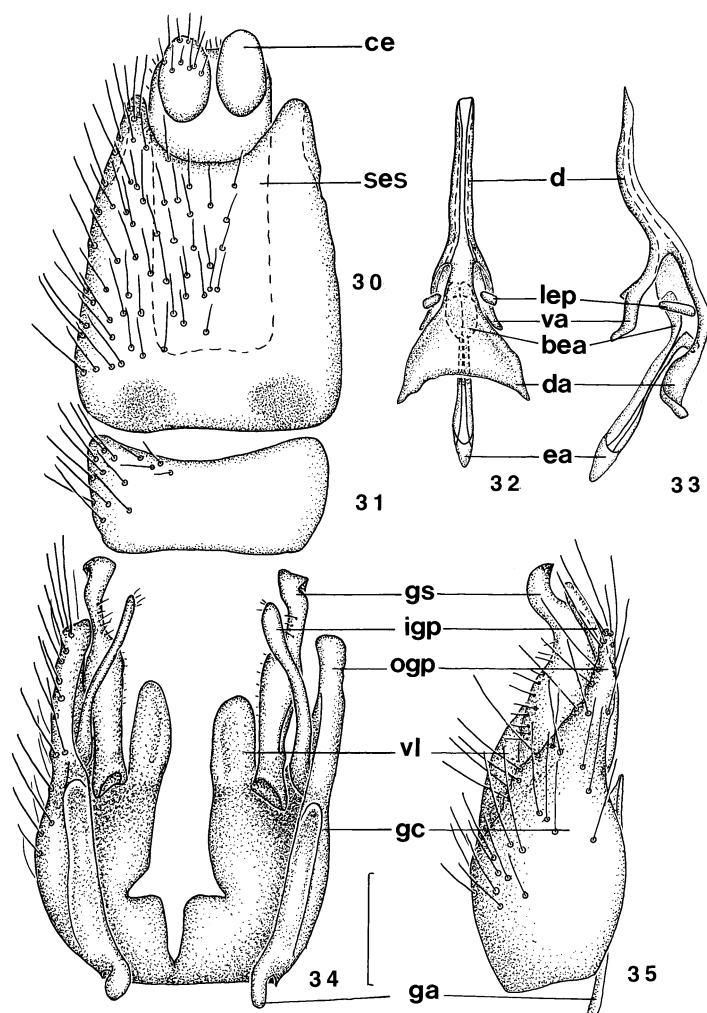
Body length: 5–6 mm. Similar to male except:

*Head.* Frons wider than ocellar tubercle, short, black setae sparsely distributed.

*Genitalia* (Figs 36–38). Furca open (i.e. not sclerotised anteriorly to complete a 'ring'); spermathecal sac simple, globose (Fig. 36); spermathecal ducts joining basally to common spermathecal sac duct; accessory glands small, symmetrical.

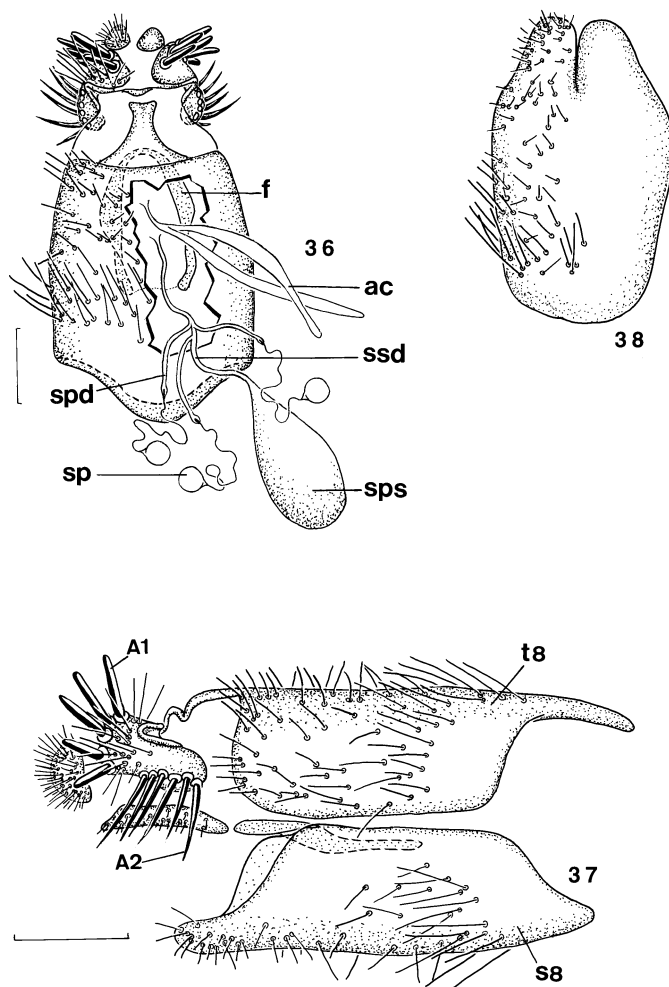
*Comments*

Completely orange body colouration is found only in *N. armeniacum* and *N. furcata*. Two rows of setae on the postocular ridge of the male is autapomorphic for *N. armeniacum*. *Nanexila armeniacum* is recorded from south-western corner of Western Australia, and Kangaroo Island, South Australia (Fig. 73). The specific epithet is derived from the Latin *armeniaceum*: apricot; pertaining to the overall body colour.



**Figs 30–35.** *Nanexila armeniacum* Winterton & Irwin, sp. nov., genitalia (♂): 30, epandrium, dorsal view; 31, tergite 8, dorsal view; 32, aedeagus, dorsal view; 33, same, lateral view; 34, gonocoxites, dorsal view with epandrium and aedeagus removed; 35, same, lateral view. Scale line: 0.2 mm.





**Figs 36–38.** *Nanexila armeniacum* Winterton & Irwin, sp. nov., genitalia (♀): 36, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 37, same, lateral view; 38, sternite 8, ventral view. Scale lines: 0.2 mm.

*Nanexila carminata* Winterton & Irwin, sp. nov.

(Figs 2, 3, 39–47, 73)

*Material examined*

*Holotype.* ♂, South Australia: 14 km NNW of Yalata Mission, 31°22'S, 131°47'E, 9.iv.1983, E.S. Nielsen & E.D. Edwards (MEI#028761) (ANIC). Condition: good.

*Paratypes.* **South Australia:** ♂, 2 ♀, same data as holotype (MEI#028762–4) (ANIC).

*Diagnosis*

Darkened tentorial pits; enlarged ventral lobe; male gonostylus with ventral comb; female accessory glands and spermathecal sac simple.

*Description*

*Male*

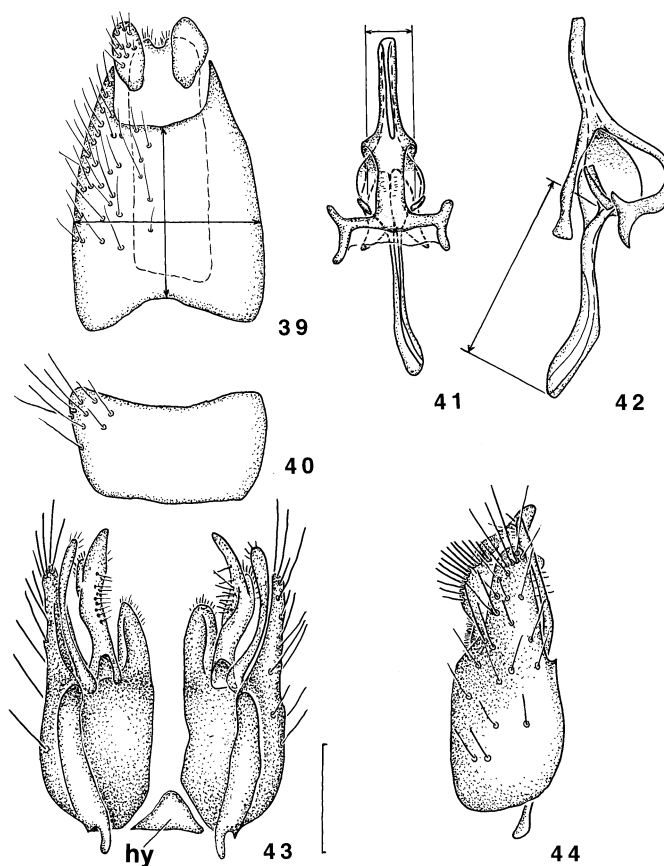
Body length: 4 mm.

**Head (Fig. 2).** Frons brown-silver pruinose, area around tentorial pits dark brown; ocellar tubercle silver pruinose, small black setae; eyes contiguous with very slight transverse furrow, facets in upper section larger than facets in lower; occiput light brown-silver pruinose; postocular ridge with a single row of setae; gena silver pruinose with fine dark setae; palps small, pale; antennae brown; scape and pedicel silver pruinose with small, dark setae; flagellum without setae, darkened distally.

**Thorax.** Scutum brown, silver pruinose, scattered small dark setae, sometimes with dark brown markings; postpronotum pale brown; scutellum dark brown, margin pale; pleuron and coxae dark brown, silver pruinose; pteropleural callus setae pale; coxal setae dark; hind coxa with single seta; legs pale yellow; wing hyaline, venation pale; haltere knob cream-coloured, stem white. Scutal chaetotaxy: np 3; sa 1; pa 1; dc 3; sc 1.

**Abdomen.** Abdomen dark brown, segments pale laterally and posteriorly; intersegmental membranes pale; long pale hairs laterally on segments 1–4; terminalia pale.

**Genitalia (Figs 39–44).** Epandrium elongate, posterolateral corners produced posteriorly; width to length ratio: 1.09; subepandrial sclerite emarginate posteriorly; tergite 8 broad; gonocoxites separate medially; hypandrium separate from gonocoxites, located anteriorly; ventral lobe enlarged, apical setae present; gonostylus modified with ventral ridge bearing a series ('comb') of ventrally directed setae, medial setae present; inner gonocoxal process narrow, apical setae present; distiphallus narrow, straight; dorsal apodeme forked, arms curved



**Figs 39–44.** *Nanexila carminata* Winterton & Irwin, sp. nov. genitalia (♂): 39, epandrium, dorsal view; 40, tergite 8, dorsal view; 41, aedeagus, dorsal view; 42, same, lateral view; 43, gonocoxites, dorsal view with epandrium and aedeagus removed; 44, gonocoxites, lateral view. Scale line: 0.2 mm.

downwards over basiphallus, secondarily forked apically; ventral apodeme forked; *bea* width to length ratio: 0.23.

#### *Female*

Body length: 5 mm. Similar to male except:

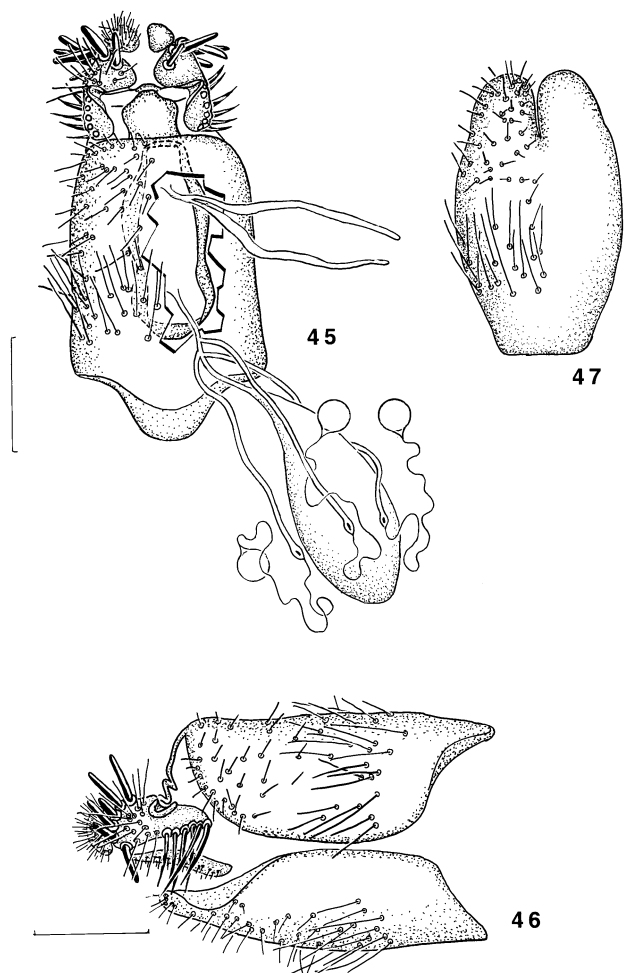
*Head* (Fig. 3). Eyes widely separated by more than twice the width of the ocellar tubercle; eye facets uniform size; frons wrinkled with small black setae; postocular ridge with two rows of setae.

*Abdomen.* Abdominal setae on segments 2–7 small, black.

*Genitalia* (Figs 45–47). Furca closed; spermathecal sac simple, ovate; duct short, straight; accessory glands symmetrical, unmodified.

#### *Comments*

The comb on the male gonostylus is autapomorphic for *N. carminata*. All specimens were collected from South Australia (Fig. 73). The specific epithet is derived from the Latin *carmino*: card, comb; referring to the ‘comb’-like arrangement of setae on the ventral edge of the gonostylus.



**Figs 45–47.** *Nanexila carminata* Winterton & Irwin, sp. nov., genitalia (♀): 45, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 46, same, lateral view; 47, sternite 8, ventral view. Scale lines: 0.2 mm.

*Nanexila furcata* Winterton & Irwin, sp. nov.

(Figs 48–55, 73)

*Material examined*

*Holotype*. ♂, South Australia: 40 miles E Nullarbor, 18.iii.1968, I.F.B. Common & M.S. Upton (MEI#028740) (ANIC). Condition: poor, head and genitalia in genitalia vial attached to pin, most of right wing missing.

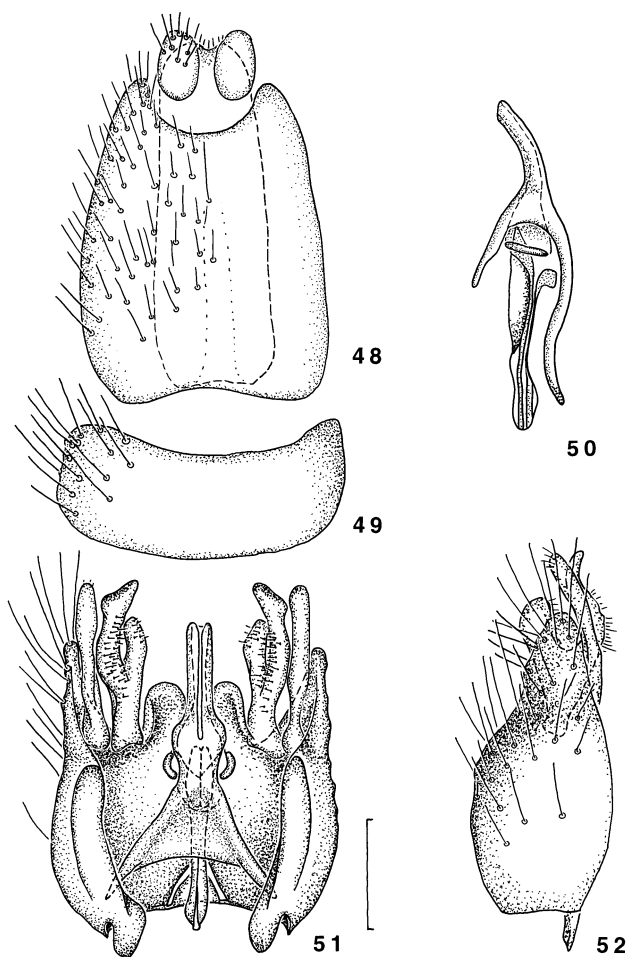
*Paratype*. **Western Australia**: ♀, 63 km E by W [?] of Norseman, 32°04'S, 122°25'E, 12.iv.1983, E.S. Nielsen & E.D. Edwards (MEI#028741) (ANIC).

*Diagnosis*

Body colouration orange; coxal setae pale, single lateral seta on hind coxa, gonostylus forked; trilobate spermathecal sac arrangement.

*Description*

Similar to *N. armeniacum* except:



**Figs 48–52.** *Nanexila furcata* Winterton & Irwin, sp. nov. genitalia (♂): 48, epandrium, dorsal view; 49, tergite 8, dorsal view; 50, aedeagus, lateral view; 51, gonocoxites and aedeagus, dorsal view with epandrium removed; 52, same, lateral view. Scale line: 0.2 mm.

*Male*

Body length: 6 mm.

*Head.* Eye facets in upper section larger than those in lower; postocular ridge with single row of black setae.

*Thorax.* Thorax integument colour pale orange, golden pruinose; unpatterned; coxal setae pale. Scutal chaetotaxy: np 3; sa 1; dc 3; pa 1; sc 1.

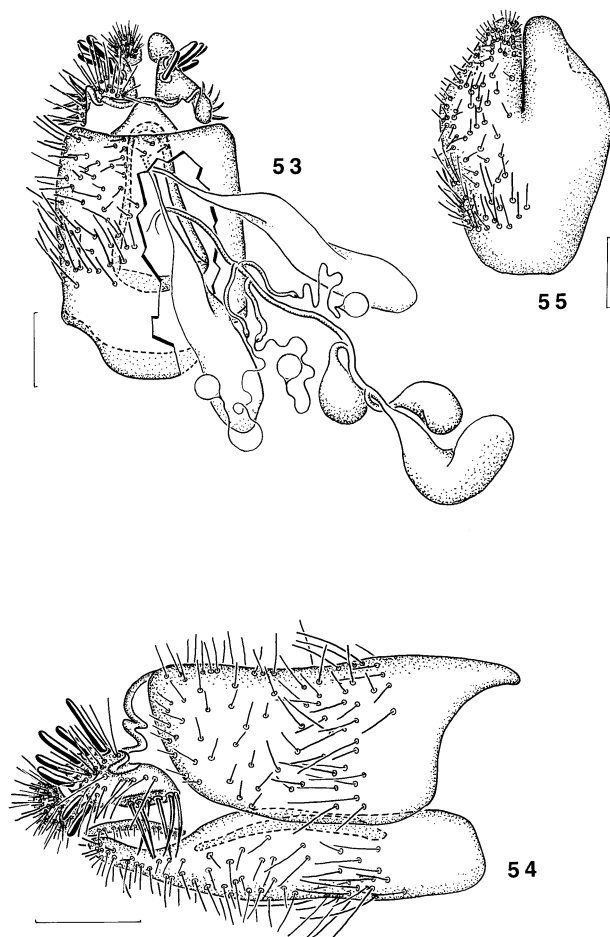
*Abdomen.* Colour pale yellow.

*Genitalia (Figs 48–52).* Epandrium width to length ratio: 0.95; gonocoxites separate; hypandrium separate from gonocoxites; gonostylus forked, dorsal fork sclerotised distally; distiphallus curved ventrally; ventral apodeme simple; *bea* width to length ratio: 0.47.

*Female*

Body length: 8 mm.

*Genitalia (Figs 53–55).* Furca closed; spermathecal sac trilobate, single median sac with two smaller sacs laterally, sacs globose; spermathecal ducts joining basally to common spermathecal sac duct; accessory glands large, symmetrical.



**Figs 53–55.** *Nanexila furcata* Winterton & Irwin, sp. nov., genitalia (♀): 53, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 54, same, lateral view; 55, sternite 8, ventral view. Scale lines: 0.2 mm.

*Comments*

*Nanexila furcata* is closely related to *N. armeniacum*, and is separable by the presence of a single row of setae on the postocular ridge and forked gonostylus of the male, trilobate spermathecal sacs in the female and pale coxal setae. The forked gonostylus is autapomorphic for the species. The overall colouration of *N. furcata* is slightly paler than *N. armeniacum*. *Nanexila furcata* is recorded from south-western Australia (Fig. 73). The specific epithet is derived from the Latin *furca*: forked, pitchfork; referring to the forked gonostylus of the male.

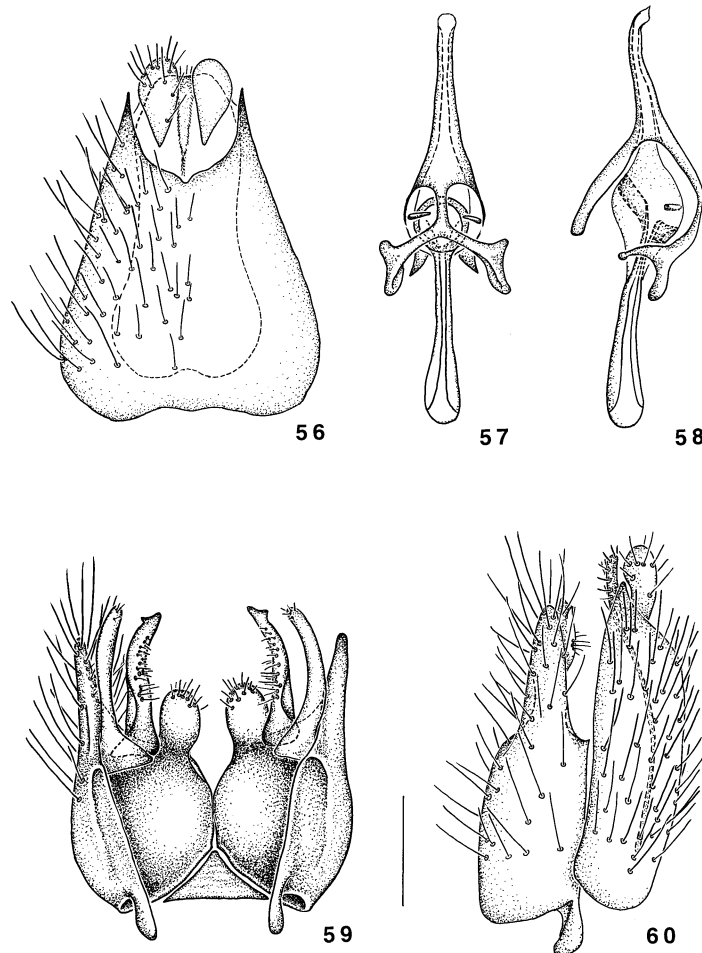
*Nanexila manni* (Hardy, 1955), comb. nov.

(Figs 5, 56–63, 73)

*Anabarhynchus manni* Hardy, 1955: 178, Figs 2–4.*Material examined**Holotype*. ♂, New South Wales: Katoomba, 2.xii.1952 (MEI#029220) (AM). Condition: good.*Allotype*. **New South Wales**: ♀, Katoomba, 3.xii.1953, G.H. Hardy (MEI#029227) (AM).

*Other material examined*. **Queensland**: ♂, Brisbane Forest Pk, top of scrub road (Site 4), 27°25'11"S, 152°50'51"E, 6–9.xi.1995, M.E. Irwin, S.D. Gaimari, ex: Focks malaise trap (MEI#027476) (IRWC); ♂, Mt Glorious, 27°19'S, 152°45'E, 1–14.iv.1996, 700 m amsl, A. Hillier, G. & A. Daniels, malaise trap (MEI#090746) (UQIC); ♂, ♀, Isla Gorge Natl Pk (25°11'S, 149°58'E), 320 m, 12.ix.1993, G. & A. Daniels, mv lamp (MEI#033670, 33855) (GDCB); 3♂, 3♀, Isla Gorge Natl Pk, 25°11'S, 149°58'E, 320 m, 13.ix.1993, G. & A. Daniels, mv lamp (MEI#033669, 33671–2, 33859–61) (GDCB); 2♂, ♀, Isla Gorge Natl Pk, 25°11'S, 149°58'E, 320 m, 3.x.1993, G. & A. Daniels, mv lamp (MEI#033673, 33854, 33858) (GDCB); ♀, Isla Gorge Natl Pk, 25°11'S, 149°58'E, 320 m, 3.iii.1993 G. & A. Daniels, mv lamp (MEI#028770) (GDCB); ♂, 5 km S Leyburn, 27°58'S, 151°38'E, 450 m, 6.xi.1993, G. & A. Daniels, mv lamp (MEI#033853) (GDCB); ♀, Maranoa River, West Branch, Mt Moffatt sect., Carnarvon Natl Pk, 25.ix.1986, D.K. Yeates, malaise trap (MEI#028670) (UQIC); ♀, Maranoa River, West Branch, Mt Moffatt sect., Carnarvon Natl Pk, 24–26.ix.1995, M.E. Irwin & S.D. Gaimari, Focks malaise trap (MEI#031024, 31522) (IRWC); **New South Wales**: ♀, Apsley Falls, nr Walcha, 975 m, 30.xi.1962, E.S. Ross & D.Q. Cavagnaro (MEI#028673) (CAS); ♀, 5 km SE Broadwater (site 2), 29°01'45"S, 153°28'26"E, Irwin, Yeates, Gaimari, 5.xi.1995 (MEI#031262) (UQIC); ♀, Hornsby, 28.ix.1950, B. McMillan (MEI#090747) (UQIC); ♀, Mt Kaputar Natl Pk, Lower Eulah Ck, 15.i.1994, Irwin & Yeates, malaise trap (MEI#028703) (IRWC); ♀, Katoomba, Dec. 1949, G.H. Hardy (MEI#029211) (AM); ♀, Katoomba, 21.x. 1955, G.H. Hardy (MEI#028668) (ANIC); ♀, Katoomba, 2.i.1957, G.H. Hardy (MEI#029223) (AM); ♀, Katoomba, 31.x.1957, G.H. Hardy (MEI#029224) (AM); ♀, Katoomba, 23.xi.1957, G.H. Hardy (MEI#029215) (AM); ♂, Katoomba, 2.xii.1957, G.H. Hardy (MEI#028659) (AM); 2♀, Katoomba, 3.xii.1957, G.H. Hardy (MEI#029219, 29221) (AM); ♀, Katoomba, 2.ii.1959, G.H. Hardy (MEI#029218) (AM); ♀, Katoomba, 3.ii.1959, G.H. Hardy (MEI#029222) (AM); ♀, Katoomba, 11.xii.1960, G.H. Hardy (MEI#029217) (AM); ♀, Katoomba, 23.xii.1960, G.H. Hardy (MEI#029226) (AM); ♀, Katoomba, 11.i.1961, G.H. Hardy (MEI#029213) (AM); ♀, Katoomba, 24.i.1961, G.H. Hardy (MEI#029212) (AM); ♀, Katoomba, 5.xi.1961, G.H. Hardy (MEI#029216) (AM); ♀, Katoomba, 4.12.1991 [April] (Frank M. Hull Collection) (MEI#027319) (CNC); ♂, Tenterfield, 11.xii.1946, R. Pullen, caught on window pane (MEI#029209) (AM); ♀, 20 miles NW Upper Colo, 8.xi.1955, T.G. Campbell (MEI#028674) (ANIC); 2♀, Urila, 26 km S Queanbeyan, 1–10.xii.1987, M.E. Irwin, ex. malaise trap (MEI#028671–2) (UQIC); ♂, ♀, Wahroonga, Sydney, 24.x.1926, J. Mann's coll. (MEI#028656, 28669) (ANIC); ♀, Waratah Trig Track, Gibraltar Range Natl Pk, 29°30'S, 152°15'E, 17.xii.1996, D.K. Yeates, S.L. Winterton & C. Lambkin, ex. malaise trap (UQIC); ♀, 2 km W Wardell (site 1), 28°54'22"S, 147°50'37"E, 4–5.xi.95, Gaimari, Irwin & Yeates, ex: in coastal scrub, heath on sandy substrate (MEI#031480) (IRWC); ♂, 2♀, Warumbungle Natl Pk, Woolshed, Wombelong Ck, 24–29.xii.1992, M.E. Irwin (MEI#028694, 28697, 28702) (IRWC); 2♂, 4♀, Warumbungle Natl Pk, Buckleys Ck, 1.7 km N Camp Blackman, 480 m, 23–30.xii.1992, M.E. Irwin (MEI#028693, 28695–6, 28699–701) (IRWC); ♂, ♀, Warumbungle Natl Pk, Buckleys Ck, 1.7 km N Camp Blackman, 480 m, 2 January 1993, M.E. Irwin (MEI#028693, 28698) (IRWC); 2♂, 6♀, Warumbungle Natl Pk, Buckleys Ck, 1.5 km NE Blackman camp, 17.xii.1995, M.E. Irwin (MEI#051702, 51360, 51516, 51771, 51692, 51464, 51125, 51467) (IRWC); 2♀, Warumbungle Natl Pk, Buckleys Ck, 1.5 km NE Blackman camp, 17.xii.1995, M.E. Irwin malaise trap (MEI#046271, 49424) (IRWC); ♀, K62656, collection data unknown, B. Bertram collection (MEI#029210); 6♂, 22♀, Warumbungle Natl Pk, Browns Ck, 2.5 km N Woolshed, 17.xii.1995, M.E. Irwin, collected in malaise trap (MEI#041132, 41224, 41468, 41525, 41688,

42178, 42188, 42195, 43335, 43342, 43345, 43363, 44405, 44416, 45469, 46271, 46293, 46328, 46349, 46362, 46367, 46376, 46386, 48728, 48733, 49181, 49391, 49424) (IRWC); 2♂, Warumbungle Natl Pk, Wombelong Ck at Woolshed, 27.xii.1987, M.E. Irwin (MEI#028660–1) (QM); ♀, Warumbungle Natl Pk, Browns Ck nr Wombelong Ck, 31°16'24"S, 148°57'38"E, 17.xii.1995, M.E. Irwin, near cliff overhang at water hole (MEI#050979) (IRWC); **Australian Capital Territory**: ♂, Black Mtn, 17.xii.1957, I.F.B. Common, light trap (MEI#028655) (ANIC); ♂, Black Mtn, 19.xii.1957, I.F.B. Common, light trap (MEI#028658) (ANIC); ♂, Black Mtn, 35°16'S, 149°06'E, 600 m, 15–21.i.1988, M.E. Irwin, malaise trap (MEI#028657) (IRWC); **Victoria**: Cathedral Range S.P., 20.viii.1983, M.E. Irwin [collected as larvae; pupated 2.x.1983; eclosed 19.x.1983] (MEI#028664) (IRWC); **Western Australia**: ♀, Palmyra, 18.i.1989, B.E. Heterick, at verandah light (MEI#028675) (WADA); ♀, Perth, 6.iii.1942, P.N.F. (MEI#028689) (WADA); ♀, Perth 14.iii.1945, P.N.F. (MEI#028690) (WADA); ♂, ♀, Mt Claremont, Perth, 10.iv.1968, I.F.B. Common & M.S. Upton (MEI#028687, 28663) (ANIC); ♀, Nedlands, 1.iii.1965, D.L. Serventy (WAM); 2♀, Kalmunda Natl Pk, 16.xi.1987, E.I. Schlinger & M.E. Irwin, malaise trap (MEI#028679–80) (UQIC); 2♀, Walyunga Natl Pk, 5.xi.1987, M.E. Irwin & E.I. Schlinger, malaise trap (MEI#028678, 28683) (UQIC); 4♀, Walyunga Natl Pk, 10–16.xi.1987, M.E. Irwin & E.I. Schlinger, malaise trap (MEI#028677, 28681–2, 28684) (UQIC); ♀, Walyunga Natl Pk, 16.xi.1987, M.E. Irwin & E.I. Schlinger (MEI#028676) (UQIC); ♀, Yallingup, 9.xi.1958, E.F. Riek (MEI#028688) (ANIC); ♂, ♀, Yallingup, SW WA, 30.xi.1978, M.S. & B.J. Moulds (MEI#028662, 28686) (GDCB).



**Figs 56–60.** *Nanexila manni* Winterton & Irwin, sp. nov. genitalia (♂): 56, epandrium, dorsal view; 57, aedeagus, dorsal view; 58, same, lateral view; 59, gonocoxites, dorsal view with epandrium and aedeagus removed; 60, gonocoxites and epandrium, lateral view. Scale line: 0.2 mm.

*Diagnosis*

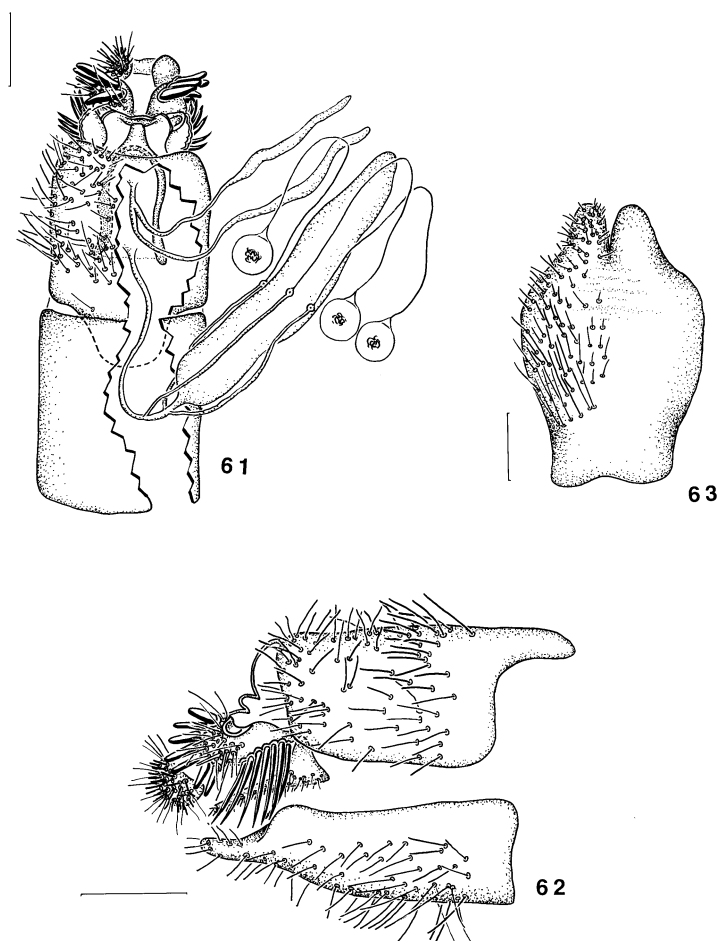
Posterolateral processes of the epandrium narrowed to a point; gonostylus simple; abdomen dark, without markings; male with faint silver pruinose abdomen; enlarged ventral lobe; spermathecal sac simple.

*Redescription**Male*

Body length: 5–6 mm.

*Head.* Frons brown, silver pruinose; face silver below level of antennal bases; eyes contiguous, facets larger in upper section than those in lower; ocellar tubercle with brown-silver pruinescence, several small dark setae; occiput and gena silver pruinose; postocular ridge with single row of black setae; palps small, pale; antennae pale with silver pruinescence; scape and pedicel with dark setae; flagellum orange, darkened distally, two to four small setae at base of first segment.

*Thorax (Fig. 22).* Scutum colouration and markings variable, markings absent in holotype, ground colour pale grey to brown pruinose, small dark setae sparsely covering scutum, markings dark brown, usually with a thin median stripe and broken lines or spots either side of line;



**Figs 61–63.** *Nanexila manni* Winterton & Irwin, sp. nov., genitalia (♀): 61, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 62, same, lateral view; 63, sternite 8, ventral view. Scale lines: 0.2 mm.



scutellum slightly darker than scutum; pleuron and coxae grey pruinose; setae on pteropleural callus pale; all thoracic macrosetae dark; hind coxa with one or two lateral setae; legs pale, terminal tarsi segment dark. Scutal chaetotaxy: np 3; sa 1; pa 1; dc 3–5; sc 1.

*Abdomen* (Fig. 22). Abdomen black, venter grey, silver pruinose laterally and ventrally, although intensity highly variable; long pale hairs laterally on segments 1–7; intersegmental membranes pale; terminalia pale brown, sometimes darkened medially.

*Genitalia* (Figs 56–60). Epandrium elongate with distinct posterolateral processes width to length ratio: 1.02; tergite 8 broad; gonocoxites separate medially; hypandrium separate from gonocoxites, located anteriorly; ventral lobe enlarged, apical setae present; gonostylus with medial and ventral setae, sclerotised apically; inner gonocoxal process narrow, apical setae present; distiphallus narrow, slightly recurved dorsally; dorsal and ventral apodemes forked, dorsal apodeme enlarged, secondarily forked distally; *bea* width to length ratio: 0.35.

### Female

Body length: 7–8 mm. Similar to male except:

*Head* (Fig. 5). Eyes widely separated by almost twice the width of the ocellar tubercle; frons slightly wrinkled with small black setae; postocular ridge with two rows of setae.

*Abdomen*. Abdomen only rarely with faint silver pruinescence; venter black; setae on segments 2–7 small, black.

*Genitalia* (Figs 61–63). Furca open; spermathecal sac simple, elongate; accessory glands symmetrical, unmodified.

### Comments

Irwin and Lyneborg (1989) listed *A. manni* Hardy as unplaced within the Therevidae, indicating that it does not belong in *Anabarhynchus*, and examination of male and female genitalia show that *Anabarhynchus* and *Nanexila* clearly belong to separate subfamilies.

The scutal markings of *N. manni* are highly variable, and the number of lateral setae on the hind coxa varies from one to two, sometimes on a single individual. *Nanexila manni* is widely distributed across eastern and southern Australia with two populations, one in eastern Australia and the other in Western Australia (Fig. 73). There is no apparent morphological differences between the two populations. Hardy (1955) collected this species sweeping along a storm-water drain and on bare cultivated ground.

### *Nanexila nana* Winterton & Irwin, sp. nov.

(Figs 4, 64–72, 73)

### Material examined

*Holotype*. ♂, Queensland: Atherton, 2.x.1959, G. Ettershank, ex. citrus (MEI#028717) (QM). Condition: good.

*Paratype*. **Queensland**: ♀, Charleville, 27.x.–5.xii.1989, P. Johnson, malaise trap (MEI#028718) (ANIC).

### Diagnosis

Epandrium without posterolateral processes; ventral lobe enlarged; female accessory glands modified; spermathecal sac simple.

### Description

Similar to *N. manni* except:

### Male

Body length: 4 mm.

*Head*. Frons brown, pruinose; antennae pale with silver pruinescence; flagellum uniform orange, setae lacking.

*Thorax.* Scutum and scutellum brown pruinose, faint pruinose stripe medially, scutal macrosetae brown; minor setae black, various lengths, sparsely covering scutum; pleuron and coxae silver pruinose, area around bases of anepisternal setae brown pruinose; hind coxa with two lateral setae; legs pale. Scutal chaetotaxy: np 3; sa 1; pa 1; dc 4; sc 1.

*Abdomen.* Abdomen dark brown, venter grey, faint silver pruinescence laterally and ventrally; intersegmental membranes pale yellow; terminalia brown.

*Genitalia* (Figs 64–69). Epandrium elongate, posterolateral processes reduced, width to length ratio: 1.0; ventral lobe large, greater than half the length of the gonostylus; weakly sclerotised apically; apical setae present; distiphallus narrow, straight; *bea* width to length ratio: 0.34.

#### *Female*

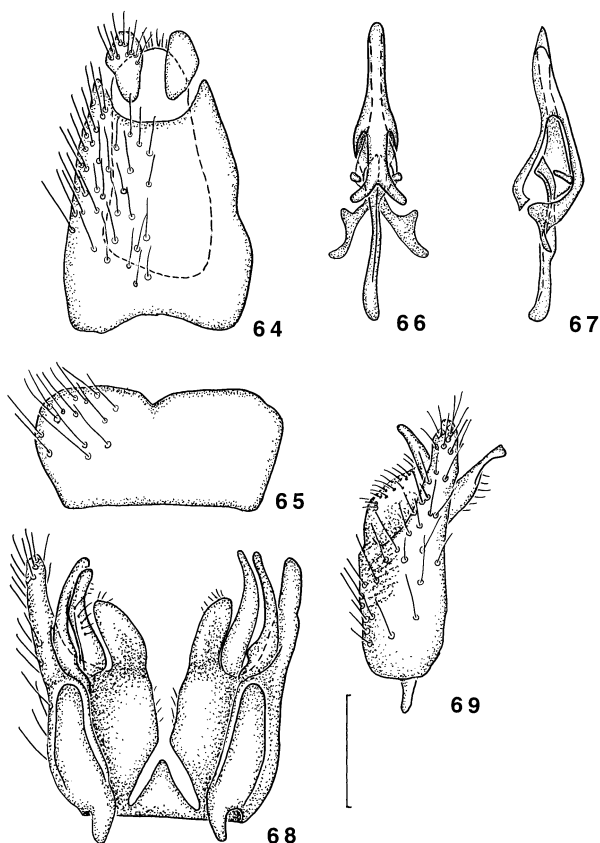
Body length: 4 mm.

*Head.* See figure 4.

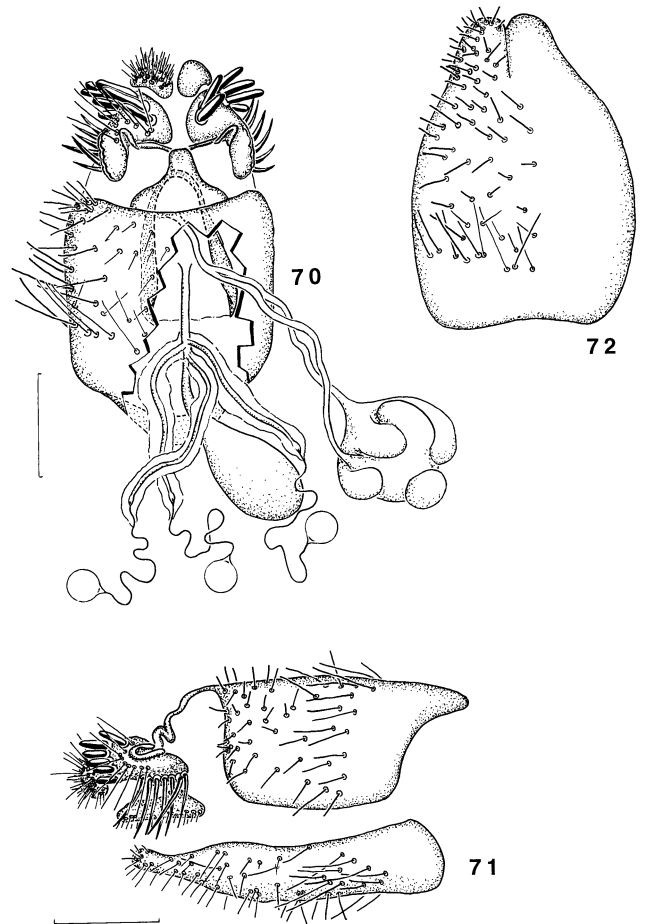
*Genitalia* (Figs 70–72). Spermathecal sac small ovate, elongate; accessory glands asymmetric, highly modified, larger gland lobate, interdigitate with smaller gland.

#### *Comments*

The male and female specimens representing this species have been associated because of morphological similarity. Both specimens are from Queensland, the male from Atherton, the



**Figs 64–69.** *Nanexila nana* Winterton & Irwin, sp. nov., genitalia (♂): 64, epandrium, dorsal view; 65, tergite 8, dorsal view; 66, aedeagus, ventral view; 67, same, lateral view; 68, gonocoxites, dorsal view with epandrium and aedeagus removed; 69, same, lateral view. Scale line: 0.2 mm.

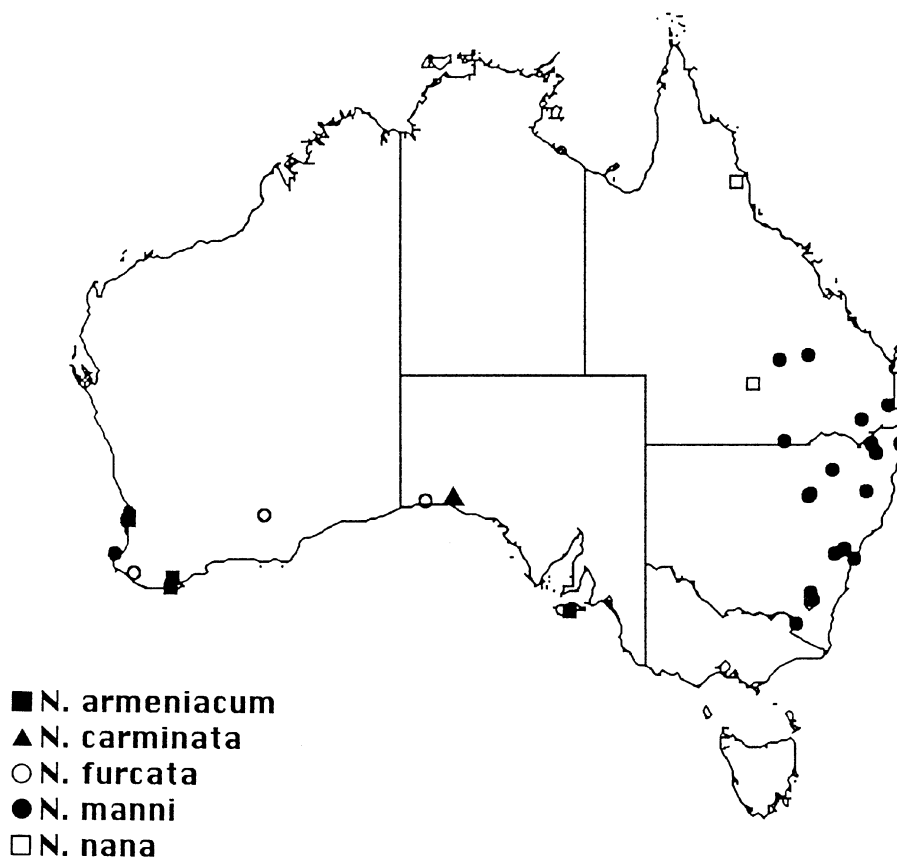


**Figs 70–72.** *Nanexila nana* Winterton & Irwin, sp. nov., genitalia (♀): 70, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 71, same, lateral view; 72, sternite 8, ventral view. Scale lines: 0.2 mm.

female from Charleville (Fig. 73). The similarity in colouration, enlarged ventral lobe and shape of the aedeagus of *N. nana*, *N. carminata* and *N. manni* suggests that the three are closely related. The greatly modified accessory glands of the female are autapomorphic for the species. The specific epithet is derived from the Latin *nanus*: a dwarf; pertaining to the small size of individuals of this species.

#### *Nanexila palassa* species-group

This species-group (clade 14) of 10 species is heterogeneous in composition but clearly united by the presence of enlarged posterolateral setae on the epandrium, and a modified patch of short setae located posteromedially on abdominal tergite 2 of the female. In all species in this group the ground colouration of the abdomen is pale yellow; although extensive tergal markings (e.g. *N. livea* Winterton & Irwin, sp. nov.) may obscure this. *Nanexila palassa*, *N. ruficornis*, *N. ligula*, *N. danielsi* and *N. spilotis* form a distinct subgroup (clade 19) characterised by a greatly enlarged base of the ejaculatory apodeme, enlarged setae arranged in series posteroventrally on the gonocoxites and a pale scutum with dark bases of the minor setae. *Nanexila argentiquadris*, *N. cylomelasma* and *N. vittata* also form a separate subgroup (clade 17) characterised by paddle-shaped arms of the ventral apodeme; uniform orange-pink or yellow



**Fig. 73.** Distribution map for *Nanexila* species; *N. manni* species-group: *N. armeniacum*, *N. carminata*, *N. furcata*, *N. manni*, *N. nana*.

colouration and a quadrate patch of metallic pruinescence located posteriorly on the scutum between the dc setae.

*Nanexila argentiquadris* Winterton & Irwin, sp. nov.

(Figs 23, 74–81, 91)

*Material examined*

*Holotype.* ♂, Western Australia: Morgan Falls, 15°02'S, 126°40'E, 16–17.viii.1975, I.F.B. Common & M.S. Upton (MEI#028706) (ANIC). Condition: good.

*Paratypes.* **Western Australia:** 2♂, 2♀, same data as holotype (MEI#028705, 28707, 28710, 28715) (ANIC); ♀, Carson Escarpment, 14°49'S, 126°49'E, 9–15.viii.1975, I.F.B. Common & M.S. Upton (MEI#028713) (ANIC); ♀, Palms Mill, N Halls Ck, 375 m, 19.x.1962, E.S. Ross & D.Q. Cavagnaro (MEI#028714) (CAS); **Northern Territory:** 2♂, ♀, 46 km SSW Borroloola, 16°28'S, 136°09'E, 28.x.1975, M.S. Upton (MEI#028708–9, 11) (ANIC); ♀, Bukalara Plateau, 46 km SSW of Borroloola, 23.iv.1976, D.H. Colless, at light (MEI#028712) (ANIC).

*Diagnosis*

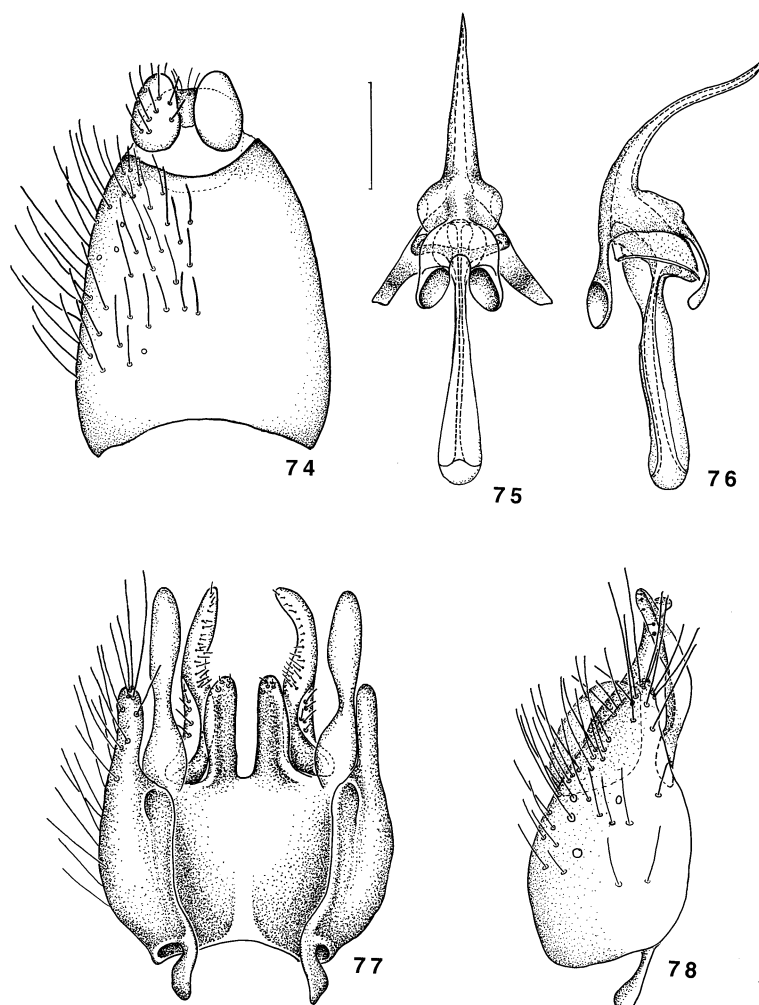
Scutum with pruinose grey quadrate patch with two arms projecting anteriorly; thoracic stripes absent; distiphallus curved dorsally; wing venation pale; trilobate spermathecal sac arrangement.

*Description**Male*

Body length: 6–7 mm.

*Head.* Frons narrow, silver pruinose, sometimes with dark vertical line medially; eyes proximate, not contiguous, facets in upper section larger than facets in lower; face and gena silver pruinose with short, dark setae on gena; palp orange-pink, unmodified; ocellar triangle and occiput silver pruinose; postocular ridge with single row of pale setae; antennal scape and pedicel silver pruinose, setae sparse, two-three dorsal setae enlarged on scape, flagellum orange, without pruinescence, distal segments dark.

*Thorax (Fig. 23).* Scutum orange-pink, silver pruinose, covered with sparse short black setae, dark quadrate patch overlain with silver-grey pruinescence located posteriorly between and bordered by dorsocentral setae; notopleural setae pale, other scutal setae dark; pteropleural setae pale; legs yellow, tarsi darkened distally; hind coxa with two lateral setae; wing hyaline, venation pale; haltere pale yellow. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 3 (rarely 4); sc 1.



**Figs 74–78.** *Nanexila argentiquadris* Winterton & Irwin, sp. nov., genitalia (♂): 74, epandrium, dorsal view; 75, aedeagus, ventral view; 76, same, lateral view; 77, gonocoxites, dorsal view with epandrium and aedeagus removed; 78, same, lateral view. Scale line: 0.2 mm.

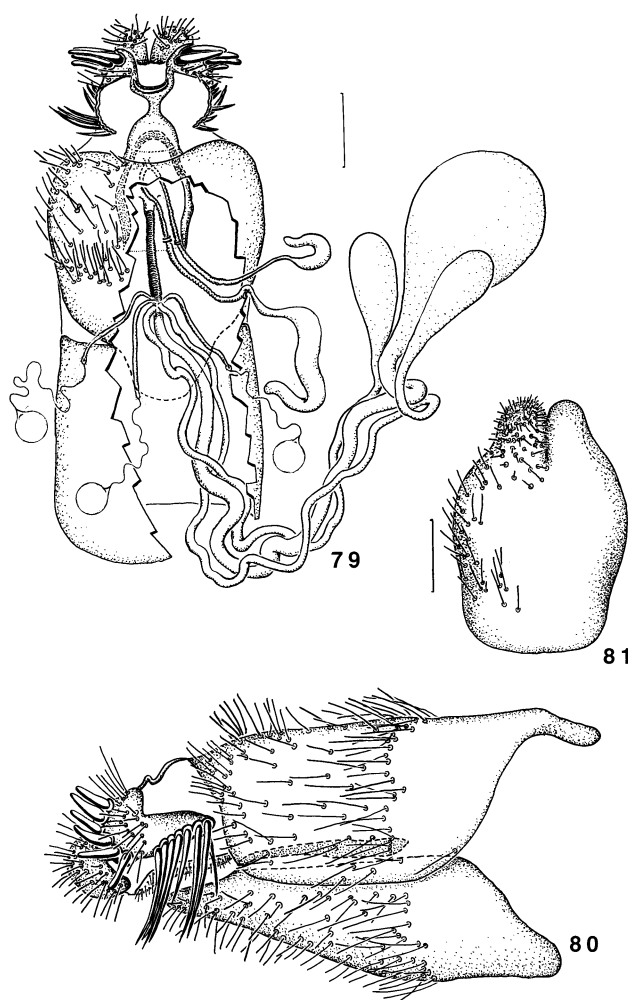
*Abdomen.* Colouration yellow, intersegmental membrane cream-white; long pale hairs laterally on each segment, tergites and gonocoxites with short, dark setae; tergites 1–2 occasionally with medial, elongate marking.

*Genitalia* (Figs 74–78). Epandrium simple, elongate, narrowed posteriorly, width to length ratio: 1.0; gonocoxites fused medially; hypandrium fused to gonocoxites; ventral lobe with setae distally; inner gonocoxal process spatulate; aedeagal complex relatively large; distiphallus recurved dorsally; ventral apodeme forked, arms paddle shaped; dorsal apodeme forked; lateral aedeagal process well developed; *bea* width to length ratio: 0.41.

#### *Female*

Body length: 7–9 mm. Similar to male except for the following:

*Head.* Frons wider than ocellar tubercle, short, black setae sparsely distributed over frons; postocular ridge with two rows of setae.



**Figs 79–81.** *Nanexila argentiquadris* Winterton & Irwin, sp. nov., genitalia (♀): 79, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 80, same, lateral view; 81, sternite 8, ventral view. Scale lines: 0.2 mm.

*Abdomen* (Fig. 23). Medial abdominal markings on tergites 1–5, markings darker than male; abdominal segments without long, pale hairs laterally, tergite 2 with modified patch of short dark setae posteromedially.

*Genitalia* (Figs 79–81). Furca open, unsclerotised anteriorly; common duct thickened; spermathecal sac trilobate, single median sac with two smaller lateral sacs; spermathecal sac ducts longer than in *N. armeniacum*, spermathecal ducts joining basally to common spermathecal sac duct; accessory glands simple, asymmetric in size.

#### Comments

This species has a northern distribution (Fig. 91), primarily in mountainous areas. Thin pruinose arms projecting anteriorly from the scutal quadrate is an autapomorphy for the species. The specific epithet is derived from the Latin *argentum*: silver; *quadrus*: square; referring to the quadrate patch of silver pruinescence on the scutum.

### *Nanexila ruficornis* (Macquart, 1850), comb. nov.

(Figs 82–90, 91)

*Anabarhynchus ruficornis* Macquart, 1850: 102—Irwin & Lyneborg, 1989: 356.

*Anabarrhynchus ruficornis* Macquart—Mann, 1928: 192 (incorrect spelling).

#### Material examined

*Syntypes*. 2♂, 3♀, Nelle Hollande (MNHN). Condition: fair.

*Other material examined*. **Queensland**: ♂, ♀, 5 km N Leyburn, 27°58'S, 151°38'E, 450 m, 17.ix.1994, G. & A. Daniels, mv lamp, in copula B (MEI#033847, 33852) (AM).

#### Diagnosis

Scutum pale with minor setal bases darkened; enlarged setae arranged in series on posteroventral surface of gonocoxites; male abdomen with bright velutum; gonocoxal apodemes short; inner gonocoxal process narrow; posterolateral processes of epandrium greatly enlarged, encircling cerci; female spermathecal sac large, elongate, quadrangular; abdominal markings present.

#### Redescription

##### Male

Body length: 7 mm.

*Head*. Frons tan, transverse silver pruinose stripe above antennal bases, brown pruinose stripe with several small dark setae above this; ocellar tubercle silver pruinose; eyes proximate, width at narrowest point slightly greater than width of anterior ocellus; eye facets in upper section slightly larger than those in lower section; occiput grey pruinose; postocular ridge brown pruinose, single row of dark setae; gena silver pruinose; palp small, pale; scape and pedicel pale yellow, pruinose with small dark setae, usually one, sometimes two enlarged dorsal and ventral setae on scape; flagellum orange; style dark.

*Thorax*. Thorax pale grey, pruinose; scutum with small dark setae sparsely distributed, setal bases dark; setae on pteropleural callus pale; legs pale, tarsi strongly darkened distally; coxal setae dark, hind coxa with two lateral setae; wing hyaline, venation dark; haltere pale yellow. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 3; sc 1.

*Abdomen*. Abdomen integument colour brown, bright blue-silver velutum; intersegmental membranes indistinct; long pale hairs laterally on segments 1–6; dark medial spots on tergites 1–5; short dark setae dorsally.

*Genitalia* (Figs 82–87). Epandrium wider than long along midline, posterolateral processes very large, encircling cerci in dry specimen, enlarged setae posterolaterally and on processes, width to length ratio: 2.06; tergite 8 broad, deeply constricted medially; gonocoxites separate medially, fused to hypandrium; anterior apodeme reduced; ventral lobe narrow, glabrous;

gonostylus with setae facing medially and ventrally; inner gonocoxal process narrow; distiphallus curved ventrally at base then straight distad; ventral and dorsal apodemes forked; base of ejaculatory apodeme enlarged, width to length ratio: 0.51.

#### *Female*

Body length: 8 mm. Similar to male except:

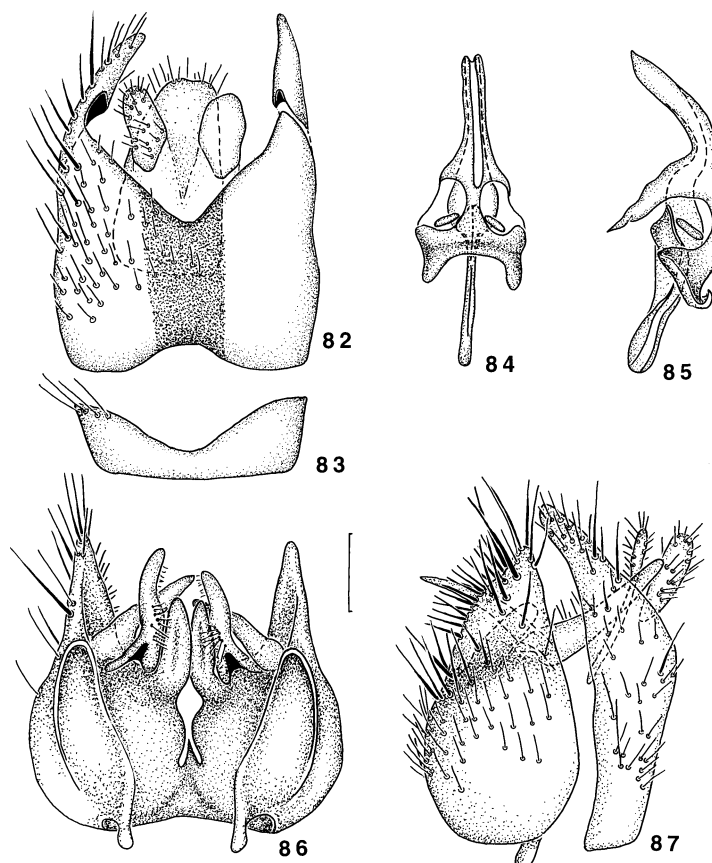
*Head.* Frons brown pruinose, numerous small dark setae; eyes widely separate, width at narrowest point greater than width of ocellar tubercle.

*Abdomen.* Abdomen without velutum or long, pale hairs laterally, segments covered with short dark setae; tergite 2 with medial patch of very short setae.

*Genitalia (Figs 88–90).* Furca closed; spermathecal sac simple, elongate, rectangular, duct very short and straight, spermathecal ducts joining basally to common spermathecal sac duct; accessory glands large, elongate.

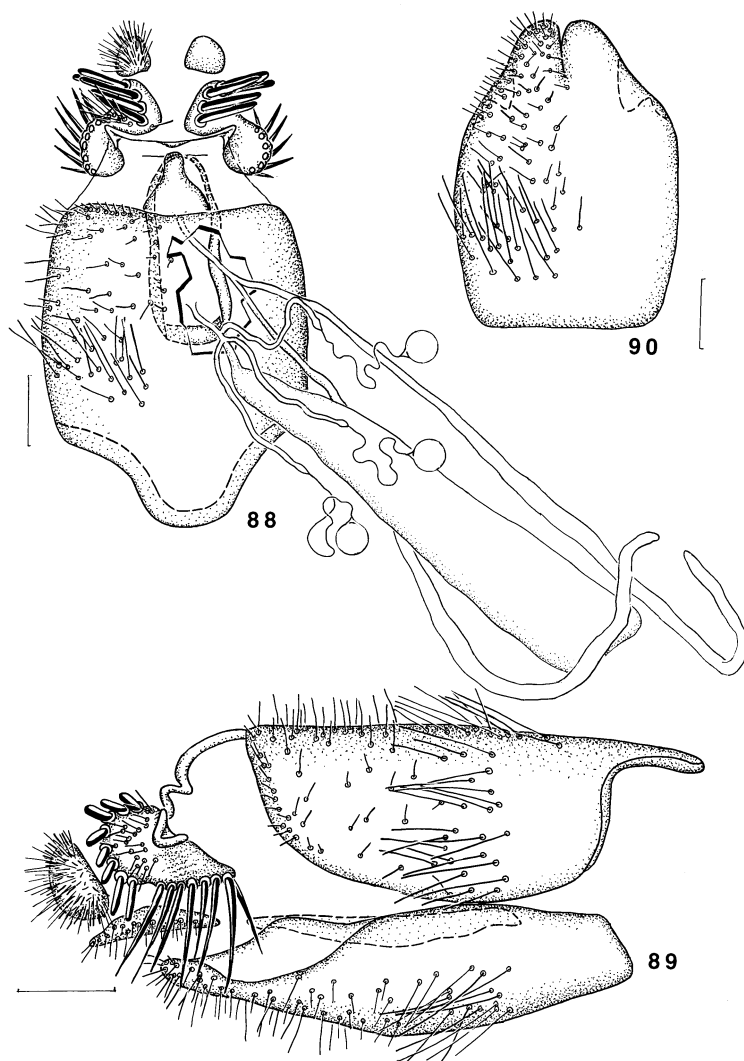
#### *Comments*

The greatly enlarged epandrial processes and large rectangular spermathecal sac make this species easily recognisable. Macquart (1850) commented on the black face; and fawn-coloured antennae are diagnostic for this species. Yet in most specimens of the type series this dark colouring of the frons is due an oily covering obscuring the underlying brown colour. Mann (1928) could not comment on the generic placement of *N. ruficornis* as he did not examine any



**Figs 82–87.** *Nanexila ruficornis* (Macquart), genitalia (♂): 82, epandrium, dorsal view; 83, tergite 8, dorsal view; 84, aedeagus, dorsal view; 85, same, lateral view; 86, gonocoxites, dorsal view with epandrium and aedeagus removed; 87, gonocoxites and epandrium, lateral view. Scale line: 0.2 mm.





**Figs 88–90.** *Nanexila ruficornis* (Macquart), genitalia (♀): 88, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 89, same, lateral view; 90, ventral view. Scale lines: 0.2 mm.

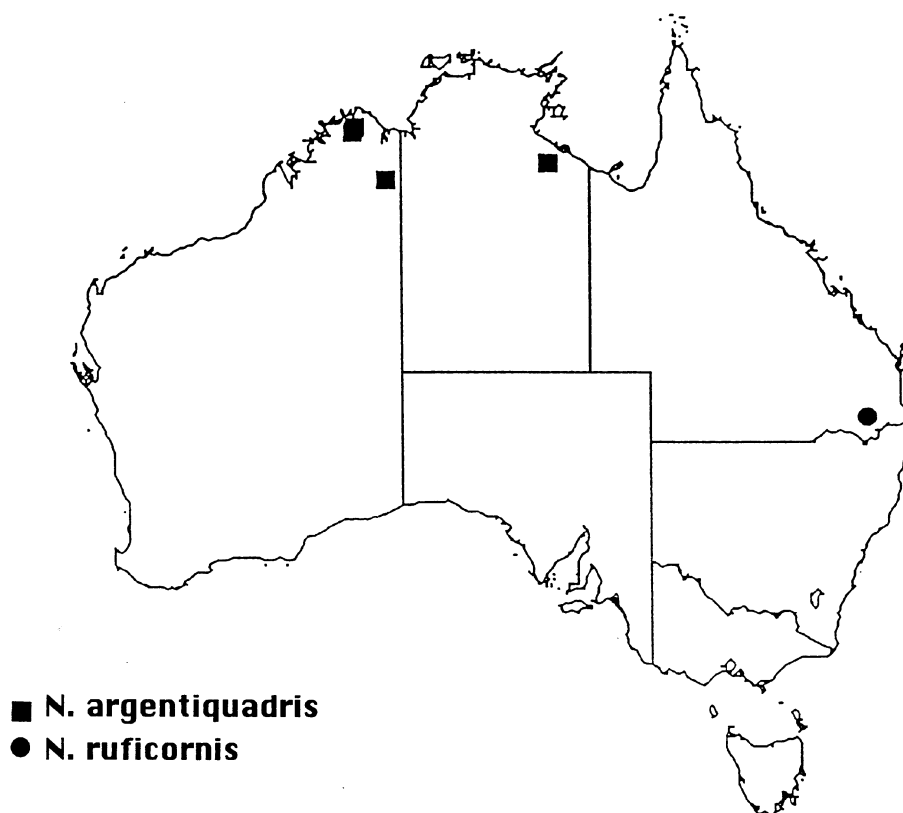
specimens of this species, yet Irwin and Lyneborg (1989) supported its placement in *Anabarhynchus*. The presence of three spermathecae in the female, a single row of postocular setae and near contiguous eyes in the male, and various male genitalic characters clearly places this species in *Nanexila*. This species is known only from the type series and a pair in copula from Leyburn, south-eastern Queensland (Fig. 91).

***Nanexila cyclomelasma* Winterton & Irwin, sp. nov.**

(Figs 8, 9, 24, 92–100, 128)

*Material examined*

*Holotype.* ♂, Western Australia: Drysdale River, 15°02'S, 126°55'E, 3–8.viii.1975, I.F.B. Common & M.S. Upton (MEI#028752) (ANIC). Condition: good.



**Fig. 91.** Distribution map for *Nanexila* species; *N. palassa* species-group: *N. argentiquadrus*, *N. ruficornis*.

*Paratypes.* **Queensland:** ♂, Little Laura River, 'Jowalbinna', 15°46'S, 144°14'E, 8.v.1989, G. & A. Daniels, mv lamp (MEI#028768) (GDCB); **Western Australia:** ♂, same data as holotype (MEI#028753) (ANIC); ♂, ♀, Carson Escarpment, 14°49'S, 126°49'E, 9–15.viii.1975, I.F.B. Common & M.S. Upton (MEI#028743, 28750) (ANIC); **Northern Territory:** ♀, Baroalba Ck Springs, 19 km ENE Mt Cahill, 28.x.1972, D.H. Colless (MEI#028749) (ANIC); 2♂, ♀, Cooper Ck, 11 km SW Nimbuwah Rock, 1.xi.1972, D.H. Colless (MEI#028746–47, 28751) (ANIC); 2♂, Cooper Ck 19 km SE Mt Borradaile, 9.xi.1972, D.H. Colless (MEI#028744–45) (ANIC); ♂, ♀, Rimbija Is., Wessel IIs, 11°01'S, 126°45'E, 19–20.i.1977, E.D. Edwards (MEI#028742, 28754) (ANIC); ♀, Rimbija Is., Wessel IIs, 11°01'S, 136°45'E, 3–14.ii.1977, T.A. Weir (MEI#028748) (ANIC).

#### *Diagnosis*

Two black spots between eyes; pruinose quadrangle on scutum; four pairs of notopleural setae; one pair of supra-alar setae; three dorsocentral setae with anterior pair greatly reduced; epandrium with a single enlarged posterolateral seta; aedeagus with distiphallus straight, arms of ventral apodeme paddle shaped; spermathecal sac simple.

#### *Description*

##### *Male*

Body length: 6–8 mm.

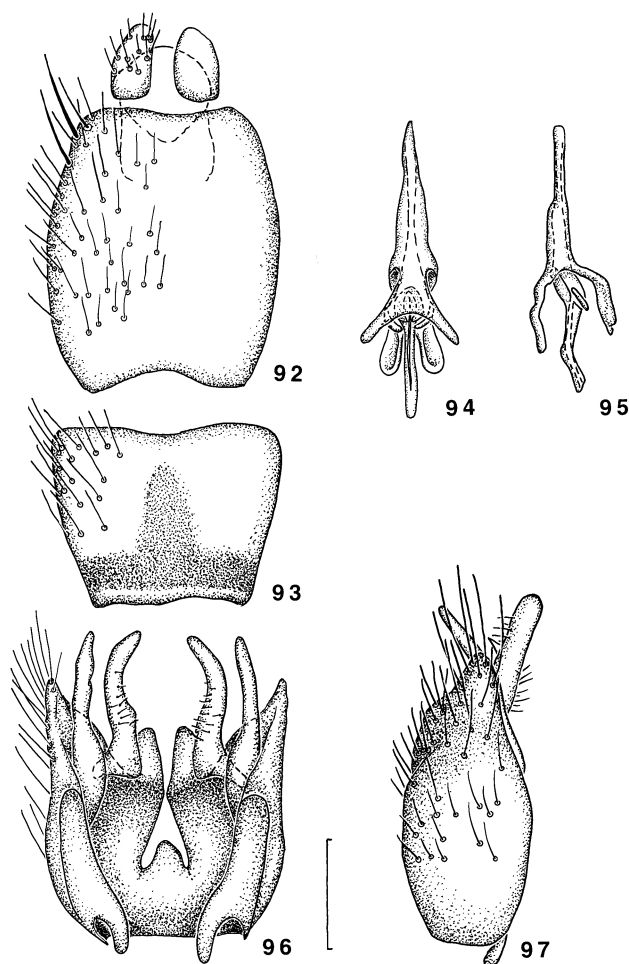
*Head* (Fig. 8). Frons silver pruinose; distinctive dark spot beneath eye encompassing tentorial pits; transverse pruinose line across face at level of antennal bases; eyes contiguous or nearly so; facets in upper section larger than those in lower; ocellar tubercle silver pruinose; occiput and gena silver pruinose, thin medial line extending vertically from ocellar tubercle;

postocular ridge with single row of pale setae; palp and labellum pale; antennae pale, silver pruinose; scape and pedicel with pale setae; flagellum orange, dark distally.

**Thorax (Fig. 24).** Thorax pale orange colour with silver pruinescence; scutum with small dark setae, slightly longer laterally; silver pruinose quadrate located posteriorly on scutum; all thoracic macrosetae pale; setae on pteropleural callus pale; legs pale, tarsi slightly darkened distally; hind coxa with two lateral setae; wing hyaline, venation pale; haltere pale orange. Scutal chaetotaxy: np 4; sa 1; pa 1; dc 3 (anterior seta minute); sc 1.

**Abdomen (Fig. 24).** Abdomen pale yellow; sometimes dark medial spots on tergites 2–5, intersegmental membranes 2–4 pale, others indistinct; segments with long pale hairs laterally and shorter black setae dorsally.

**Genitalia (Figs 92–97).** Epandrium elongate, slightly emarginate anteriorly, single enlarged setae on posterolateral corner; width to length ratio: 0.9; tergite 8 very long; hypandrium fused to gonocoxites; ventral lobe glabrous; gonostylus simple, setae directed medially and ventrally, apex weakly sclerotised; inner gonocoxal process narrow, glabrous; distiphallus straight; ejaculatory apodeme small; dorsal and ventral apodemes enlarged, forked; arms of ventral apodeme paddle shaped, *bea* width to length ratio: 0.47.



**Figs 92–97.** *Nanexila cylomelasma* Winterton & Irwin, sp. nov., genitalia (♂): 92, epandrium, dorsal view; 93, tergite 8, dorsal view; 94, aedeagus, dorsal view; 95, same, lateral view; 96, gonocoxites, dorsal view with epandrium and aedeagus removed; 97, same, lateral view. Scale line: 0.2 mm.

*Female*

Body length: 8 mm. Similar to male except:

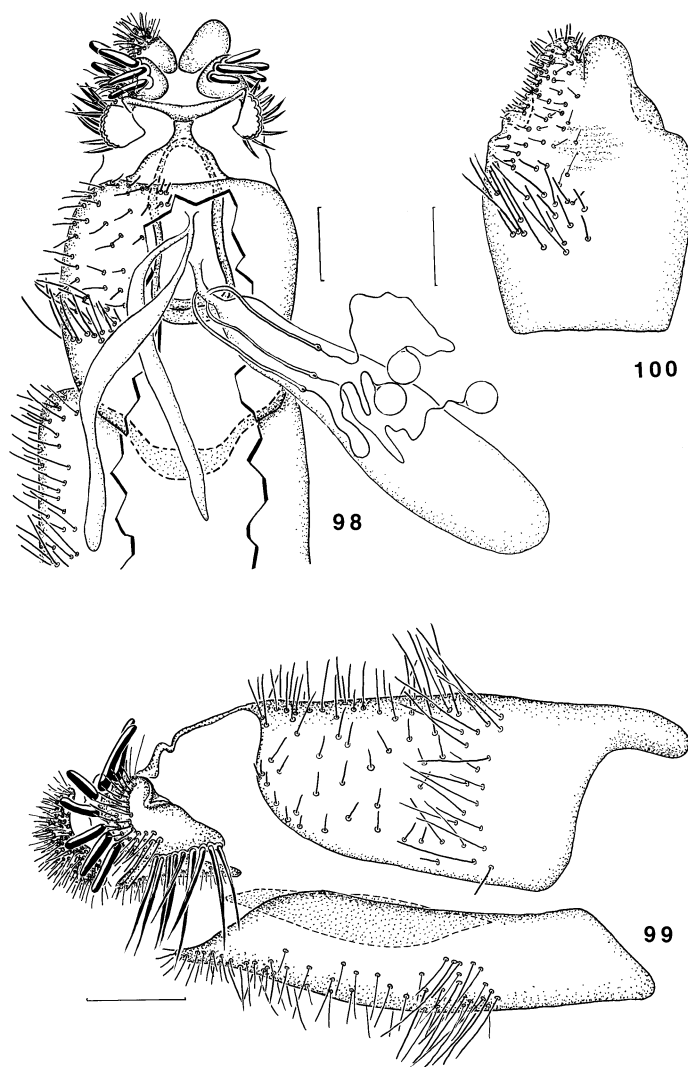
*Head* (Fig. 9). Eyes separated by distance greater than width of ocellar tubercle; two irregular rows of setae on postocular ridge.

*Abdomen.* Segments 2–8 without long pale hairs laterally, tergite 2 with a modified patch of short setae medially.

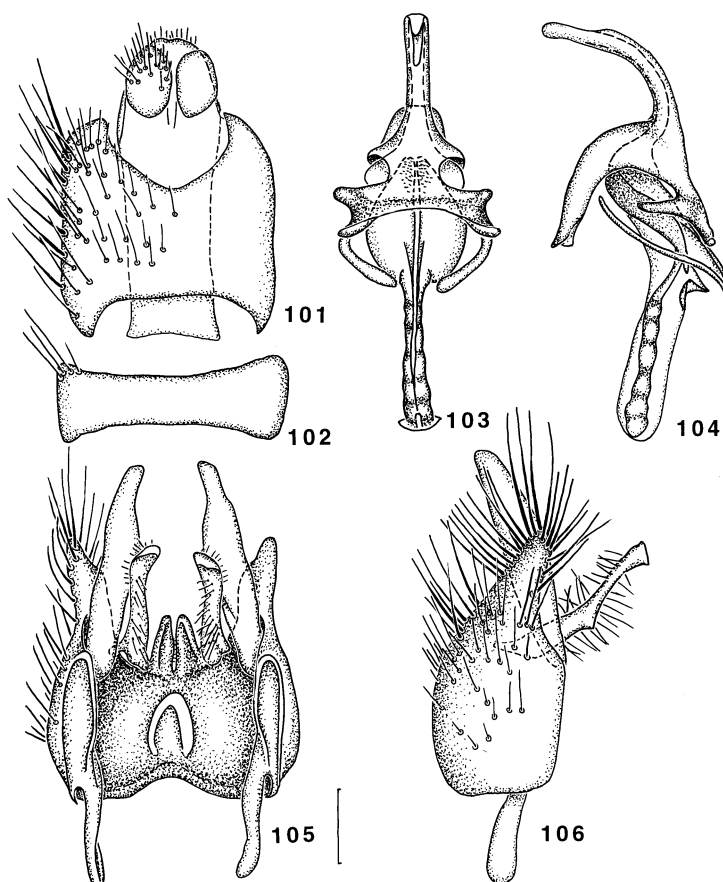
*Genitalia* (Fig. 98–100). Furca closed; sternite 8 broad, only slightly cleft apically; spermathecal sac simple, elongate, spermathecal ducts joining basally to common spermathecal sac duct; accessory glands symmetrical, unmodified.

*Comments*

*Nanexila cyclomelasma* is easily distinguished by the distinct black spots beneath the eyes. The most anterior pair of dorsocentral setae are greatly reduced and difficult to distinguish from



**Figs 98–100.** *Nanexila cyclomelasma* Winterton & Irwin, sp. nov., genitalia (♀): 98, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 99, same, lateral view; 100, sternite 8, ventral view. Scale lines: 0.2 mm.



**Figs 101–106.** *Nanexila danielsi* Winterton & Irwin, sp. nov., genitalia (♂): 101, epandrium, dorsal view; 102, tergite 8, dorsal view; 103, aedeagus, dorsal view; 104, same, lateral view; 105, gonocoxites, dorsal view with epandrium and aedeagus removed; 106, same, lateral view. Scale line: 0.2 mm.

the minor setae of the thorax, but are identifiable by their larger basal sockets. The specimen from Queensland has a grey thorax while the specimens from the Northern Territory and Western Australia have an orange-pink thorax. Intensity of abdominal markings is highly variable. *Nanexila cylomelasma* has a northern distribution throughout Western Australia, Northern Territory and Queensland (Fig. 128). The specific epithet is derived from the Greek *kylon*: part under the eye; *melasma*: a black spot.

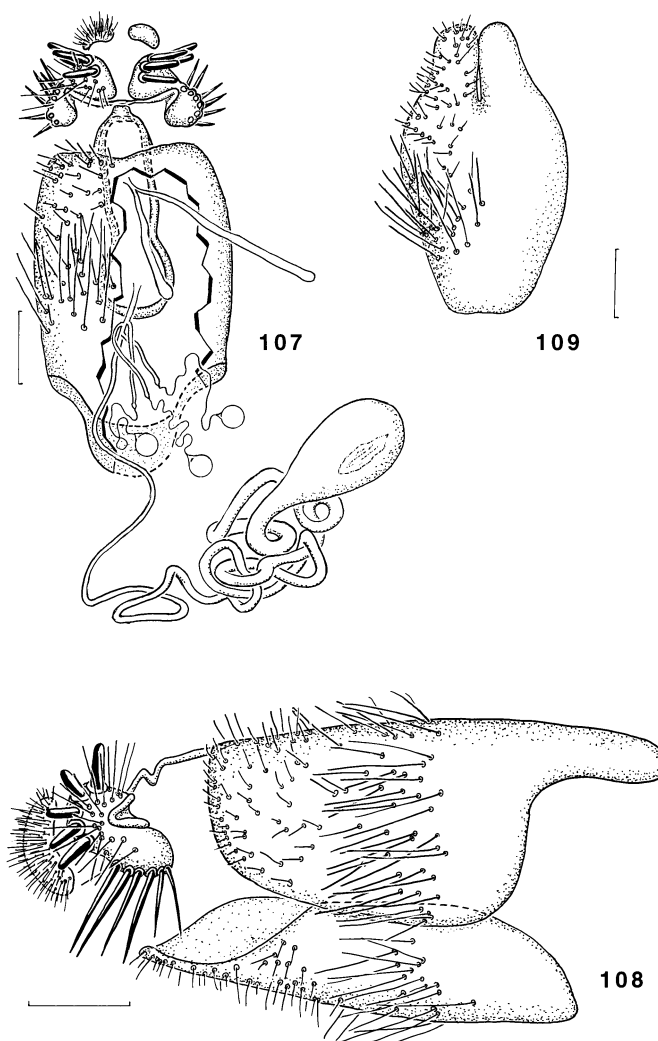
***Nanexila danielsi* Winterton & Irwin, sp. nov.**

(Figs 16, 101–109, 128)

*Material examined*

**Holotype.** ♂, New South Wales: 3 km NW Bramah H.S. [homestead], NW Balranald, 34°24'S, 143°14'E, 24.x.1983, D.C.F. Rentz & M.S. Harvey, stop 35 (MEI#029411) (ANIC). Condition: good; genitalia in genitalia vial underneath specimen.

**Paratypes.** **New South Wales:** ♀, same data as holotype (MEI#029412) (ANIC); ♂, ♀ [staged together], Round Hill Fauna Reserve, 23.x.1977, G. Daniels, mv lamp, in copula (MEI#029427–28) (GDCB); **Victoria:** 2♂, 13 km S Pirlta, 18.x.1983, J.C. Cardale, at light (MEI#029414, 29417) (ANIC); ♂, ♀, Wyperfeld Natl Pk, 4.xi.1966, I.F.B. Common & M.S. Upton (MEI#029423–24) (ANIC); 2♂, 2♀,



**Figs 107–109.** *Nanexila danielsi* Winterton & Irwin, sp. nov., genitalia (♀): 107, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 108, same, lateral view; 109, sternite 8, ventral view. Scale lines: 0.2 mm.

Wyperfeld Natl Pk, 5.xi.1966, I.F.B. Common & M.S. Upton (MEI#029419–22) (ANIC); **South Australia:** ♂, Flinders Ranges Natl Pk, Love Range Mine Rd, 31°24'06"S, 138°46'53"E; 8–10.x.1997, S. Winterton, J. & A. Skevington, C. Lambkin, malaise trap in *Callitris* and mallee lined creek bed (UQIC); 2♂, 7 km W Immarna, 7.xi.1975, J.A. Herridge, at light (SAM); 2♂, 54 km Vokes Hill Junction, 8–9.x.1976, J.A. Herridge & G.F. Gross, at light (SAM); ♂, Everard Pk Station, nr Victory Well, 2.xi.1970, G.F. Gross, ex. malaise trap (SAM); ♂, 4 miles N Colona H.S. [homestead], 20.x.1968, Britton, Upton, Balderson (MEI#029413) (ANIC); ♀, 28.5 km NW Hawker (Lake Torrens Rd), 2.x.1975, Z. Liepa (MEI#029415) (ANIC).

*Other material examined.* **Western Australia:** ♂, Buningonia Spring (Well), 31°26'S, 123°33'E, 18–25.xi.1978, T.F. Houston *et al.* (WAM); ♂, 70–75 km ENE Norseman, 10–16.xi.1978, T.F. Houston *et al.* (WAM).

#### Diagnosis

Epandrium quadrate, anteriorly and posteriorly emarginate, enlarged setae laterally; gonocoxites fused medially with hypandrium to form synsclerite; enlarged gonocoxal apodemes;

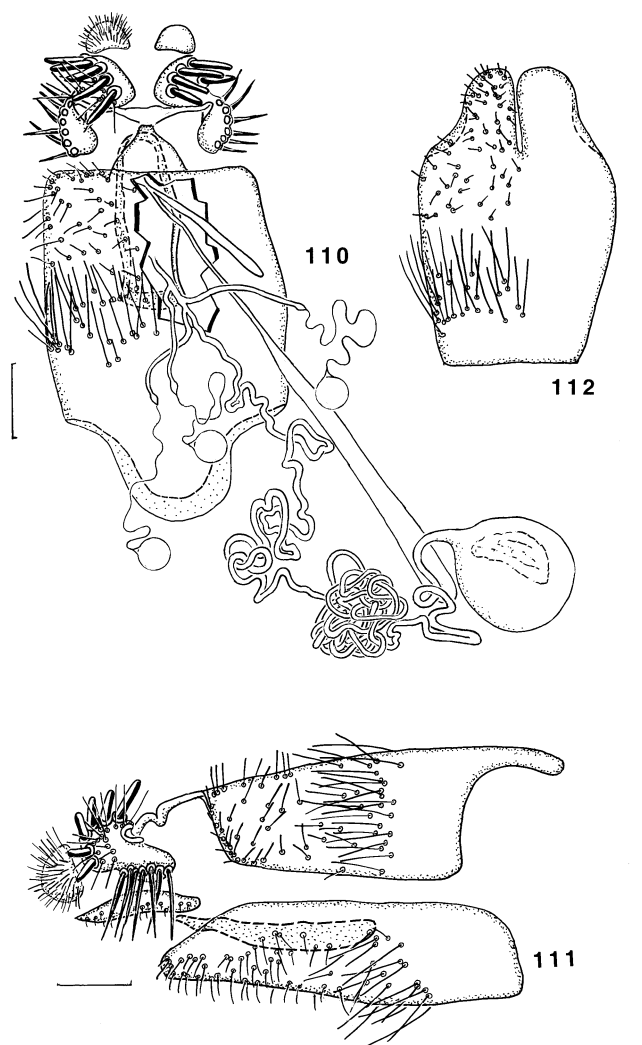
spatulate inner gonocoxal process, slightly tapered apically, apical setae absent; abdominal markings absent; subepandrial sclerite simple; spermathecal sac simple, globose; spermathecal duct long.

### Description

#### Male

Body length: 5–7 mm.

**Head.** Frons tan, silver pruinose, brown patch above antennal bases, several small dark setae above patch; ocellar tubercle black, silver pruinose; eyes proximate, width at narrowest point slightly greater than width of anterior ocellus; eye facets larger in upper section than in lower; occiput grey pruinose; postocular ridge with single row of dark setae; gena silver pruinose; palp small, pale; antennae (Fig. 16) pale yellow, silver pruinose; scape and pedicel



**Figs 110–112.** *Nanexila lignyos* Winterton & Irwin, sp. nov., genitalia (♀): 110, genitalia, dorsal view with tergite 8 part cut away to expose internal structures, spermathecal sac duct is partially teased out for clarity; 111, same, lateral view; 112, sternite 8, ventral view. Scale lines: 0.2 mm.

with small dark setae, usually one, sometimes two dorsal setae on scape enlarged; flagellum with 2–3 small dark setae basally; style dark.

*Thorax.* Scutum grey, pale yellow laterally, silver pruinose, small dark setae sparsely distributed, setal bases dark; scutellum pale yellow, pruinose, darkened anteromedially; pleuron pale yellow, pruinose, lower surface of katepisternum darkened; setae on pteropleural callus pale; legs pale, tarsi darkened distally; coxal setae dark, hind coxa with two lateral setae; wing hyaline, venation dark; haltere pale yellow, knob white to pink. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 5; sc 1.

*Abdomen.* Abdomen pale yellow; intersegmental membranes white; long pale hairs laterally on segments 1–7; short dark setae dorsally.

*Genitalia* (Figs 101–106). Epandrium broad, wider than long, emarginate anteriorly and posteriorly, enlarged setae laterally, width to length ratio: 1.92; tergite 8 short, medially constricted; gonocoxites fused medially; anterior apodeme enlarged; hypandrium fused to gonocoxites; space located anteriorly; ventral lobe narrow, setae present; gonostylus sclerotised apically, setae facing medially and ventrally; inner gonocoxal process enlarged, spatulate, slightly tapered apically; distiphallus long, curved ventrally; ventral and dorsal apodemes reduced, forked; base of ejaculatory apodeme enlarged, width to length ratio: 0.78, lateral aedeagal process enlarged.

#### *Female*

Body length: 6–8 mm. Similar to male except:

*Head.* Frons brown pruinose, silver pruinose transverse stripe just above antennal bases, small dark setae sparsely distributed; eyes widely separate, width at narrowest point greater than width of ocellar tubercle; eye facets uniform size; postocular ridge with two irregular rows of dark setae.

*Abdomen.* Abdomen without long pale hairs laterally, segments covered with short dark setae; tergite 2 with modified patch of short setae.

*Genitalia* (Figs 107–109). Furca closed; spermathecal sac simple, globose, duct long and convoluted, spermathecal ducts joining basally to common spermathecal sac duct; accessory glands symmetrical.

#### *Comments*

*Nanexila danielsi* does not have any distinctive autapomorphies, but is recognisable from the taxa described here by a combination of pale scutum with bases of minor setae darkened, subepandrial sclerite simple and gonocoxites and hypandrium fused to form a synsclerite. *Nanexila danielsi* is distributed throughout southern Australia and is active during October–November (Fig. 128). The specific epithet honours Mr Greg Daniels, who collected many specimens of *Nanexila* and other Australia Therevidae.

### *Nanexila lignyos* Winterton & Irwin, sp. nov.

(Figs 18, 110–112, 128)

#### *Material examined*

*Holotype.* ♀, Western Australia: ca. 25 km NE Bungalbin Hill, 30°24'S, 119°38'E, 11–18.ix.1979, T.F. Houston *et al.*, at light at night (87/2107) (WAM). Condition: good.

#### *Diagnosis*

Palp with terminal segment spatulate, attached to basal segment at odd angle; wing infusate; spermathecal sac duct extremely long, narrow and convolute.

#### *Description*

##### *Female*

Body length: 9 mm.



*Head.* Frons silver pruinose, brown transverse stripe above antennal bases, several small dark setae; ocellar tubercle black, silver pruinose; eyes widely separate, width at narrowest point greater than width of anterior ocellus; eye facets uniform size; occiput silver pruinose; postocular ridge with two irregular rows of dark and pale setae; gena silver pruinose; palp pale, terminal segment spatulate, attached to basal segment at an odd angle; antenna pale yellow, flagellum orange, silver pruinose; scape and pedicel with small dark setae, several dorsal setae enlarged on scape; flagellum with 2–3 small dark setae basally; style dark.

*Thorax.* Scutum grey, pale orange laterally, silver pruinose, small, sparsely distributed setae, setal bases dark; scutellum pale yellow, pruinose, small dark spot medially; pleuron pale yellow, pruinose, lower surface of katepisternum darkened; setae on pteropleural callus pale; legs pale, hind femur dark, all tarsi darkened distally; coxal setae dark, hind coxa with two lateral setae; wing infusate (Fig. 18), venation dark; haltere pale. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 3; sc 1.

*Abdomen.* Abdomen pale yellow, brown medial markings on segments 2–5; intersegmental membranes white; short dark setae on all segments, tergite 2 with modified patch of short setae.

*Genitalia* (Figs 110–112). Furca closed; spermathecal sac simple, globose, duct extremely long and narrow, convoluted into a tight, highly tracheated ‘ball’, spermathecal ducts join basally to common spermathecal sac duct; accessory glands asymmetrical.

#### *Male*

Unknown.

#### *Comments*

*Nanexila lignyos* is a large species easily separated from other species by the pale scutum and infusate wing. The unusual palpus shape and the extremely long, convolute spermathecal sac duct is also autapomorphic for the species. The spermathecal sac duct is compacted into a compact, highly tracheated ‘ball’. *Nanexila lignyos* is recorded from the type locality only, Western Australia (Fig. 128). The specific epithet is derived from the Greek *lignyos*: thick smoke; referring to the dark infuscation around the wing veins.

#### *Nanexila ligula* Winterton & Irwin, sp. nov.

(Figs 113–118, 128)

#### *Material examined*

*Holotype.* ♂, Western Australia: S.F. [?Sir Frederick] Range (MEI#029408) (ANIC). Condition: good.

*Paratypes.* **South Australia:** ♂, Great Victoria Desert, 77 km W Vokes Hill Corner, 24.viii.1980, J. Forrest (SAM); ♂, vehicle net between Waldan and Vokes Hill Cnr, 21.viii.1980, J. Forrest (SAM); ♂, Great Victoria Desert, vehicle net between 20–110 km W Vokes Hill Cnr, 28.viii.1980, J. Forrest (SAM); 2♂, Great Victoria Desert, E side Serpentine Lakes, 28°30'S, 129°01'E 26.viii.1980, J. Forrest, at light nr *Eucalyptus* on dunes (SAM); ♂, Great Victoria Desert, E side Serpentine Lakes, 28°30'S, 129°01'E, 26.viii.1980, J. Forrest, at light on sandy rise (SAM); **Western Australia:** ♂, 20 miles N Broad Arrow, 325 m, 17.xi.1962, E.S. Ross & D.Q. Cavagnaro (MEI#029409) (CAS).

#### *Diagnosis*

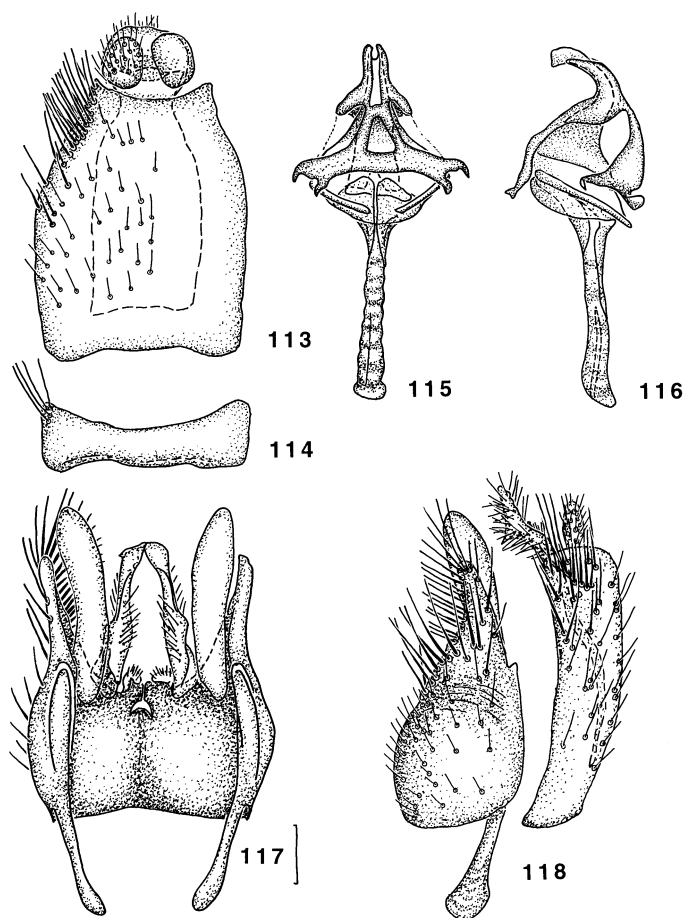
Subepandrial sclerite modified posteriorly, ladle shaped; epandrium with dense patch of enlarged setae posterolaterally; inner gonocoxal process spatulate; enlarged gonocoxal apodeme; distiphallus short.

#### *Description*

##### *Male*

Body length: 6 mm.

*Head.* Frons tan-silver pruinose, dark patch above antennal bases, several small dark setae close to patch; ocellar tubercle black, silver pruinose; eyes proximate, not contiguous, width at



**Figs 113–118.** *Nanexila ligula* Winterton & Irwin, sp. nov., genitalia (♂): 113, epandrium, dorsal view; 114, tergite 8, dorsal view; 115, aedeagus, dorsal view; 116, same, lateral view; 117, gonocoxites, dorsal view with epandrium and aedeagus removed; 118, same, lateral view. Scale line: 0.2 mm.

narrowest point greater than or equal to width of anterior ocellus; eye facets larger in upper portion than lower; occiput yellow to silver pruinose; postocular ridge with single row of dark setae; gena silver pruinose; palp small, pale; antennae pale orange, silver pruinose; scape and pedicel with small dark setae, several dorsal setae enlarged on scape; flagellum with 2–3 small dark setae basally; style dark.

**Thorax.** Scutum yellow-grey, silver pruinose, small dark setae sparsely distributed, setal bases dark; scutellum pale yellow, pruinose; pleuron pale yellow-grey, pruinose; setae on pteropleural callus pale; legs pale; coxal setae dark, hind coxa with two lateral setae; wing hyaline, venation pale; haltere pale, knob tinged with pink. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 4; sc 1.

**Abdomen.** Abdomen pale yellow, faint medial spots present on tergites 2–4; intersegmental membranes pale or indistinct; long pale hairs laterally on segments 1–7; dorsal setae short, dark.

**Genitalia (Figs 113–118).** Epandrium elongate, narrowed posteriorly; posterolateral corners with dense clump, enlarged setae, width to length ratio: 0.86; posterior margin of subepandrial sclerite modified, ladle shaped; tergite 8 short, medially constricted; anterior apodeme enlarged; hypandrium fused to gonocoxites, space located posteriorly; ventral lobe reduced, setae present; gonostylus sclerotised apically, setae facing medially and ventrally; inner gonocoxal process enlarged, spatulate; outer gonocoxal process curved slightly downwards, row

of strong enlarged setae ventrally; distiphallus short, curved ventrally; ventral and dorsal apodemes reduced, forked; base of ejaculatory apodeme enlarged, width to length ratio: 0.76, lateral aedeagal process enlarged.

#### *Female*

Unknown.

#### *Comments*

The short, ventrally curved distiphallus, modified subepandrial sclerite and dense patches of enlarged setae on the epandrium are autapomorphic for this species. *Nanexila ligula* is known only from two males collected from central Western Australia (Fig. 128), one presumably from the Sir Frederick Ranges. The specific epithet is derived from the Latin *ligula*: ladle, skimmer; referring to the shape of the subepandrial sclerite.

### *Nanexila livea* Winterton & Irwin, sp. nov.

(Figs 10, 11, 25, 119–127, 128)

#### *Material examined*

*Holotype*. ♂, Queensland: Bunya Mountains Natl Pk, 11–13.xii.1979, G. Daniels & M.A. Schneider (MEI#028755) (AM). Condition: good, left wing tip damaged.

*Paratypes*. **Queensland**: ♂, Carnarvon Natl Pk, 8–10.xii.1979, M. A. Schneider & G. Daniels (MEI#028759) (GDCB); ♀, Mt Glorious, 1.ix–17.x.1990, A. Hiller, malaise trap (MEI#028765) (ANIC); 4 ♀, Great Sandy Natl Pk, Cooloola Section, 26°02'26"S, 153°04'57"E, 1–5.x.1996, D.K. Yeates, C. Lambkin, S. Winterton, malaise trap (MEI#090719–22) (QM); 4 ♀, Great Sandy Natl Pk, Cooloola Section, 26°02'26"S, 153°04'57"E, 1–5.x.1996, D.K. Yeates, C. Lambkin, S. Winterton (MEI#090723–6) (UQIC); ♂, 2 km W Rainbow Beach, 20.xi.1986, R. Eastwood (MEI#028758) (GDCB); ♀, Mt Tamborine, Oct. 1924, A. Musgrave & C. Geissmann (MEI#029229) (AM); 2 ♂, Toowoomba, scrub below escarpment, 18.xii.1976, M.S. & B.J. Moulds (MEI#028756–7) (GDCB); ♀, Prince Henry Heights, Toowoomba, 27°33'S, 151°59'E, 620 m, 11.i.1983, I.F.B. Common (MEI#028760) (ANIC); **New South Wales**: 4 ♂, ♀, Mallanganee FR, 16 km E, Tabulam, 11.i.1988, D.J. Bickel, trunk *Eucalyptus* sp. (MEI#029228, 29230–33) (AM).

*Other material examined*. **Queensland**: 3 ♀, Mt Glorious, 19–26.ix.1979, rainforest, malaise trap (MEI#090727–29) (QDPI); ♀, Mt Tamborine, SE Qld, Marstella, 6–12.ii.1982, malaise trap (MEI#090732) (QDPI); ♂, Davidson's property homestead, Mt Tamborine, 27°57'24"S, 153°11'17"E, 9.xii.1993, K.J. Lambkin, at light (MEI#090731) (QM); ♂, Lot 22, Mt Berryman Rd, Laidley, 31.x.1990, W.F. Chamberlain, at light (MEI#026996) (TAMU); ♀, Maroochy Horticultural Research Station, Nambour, 15–22.iii.1985, malaise trap (MEI#090730) (QDPI).

#### *Diagnosis*

Trilobate spermathecal sac arrangement, sacs elongate, spermathecal ducts joined in pairs to duct of each spermathecal sac lobe; ventral lobe on outer gonocoxal process of gonocoxites; distiphallus long, sharply recurved ventrally.

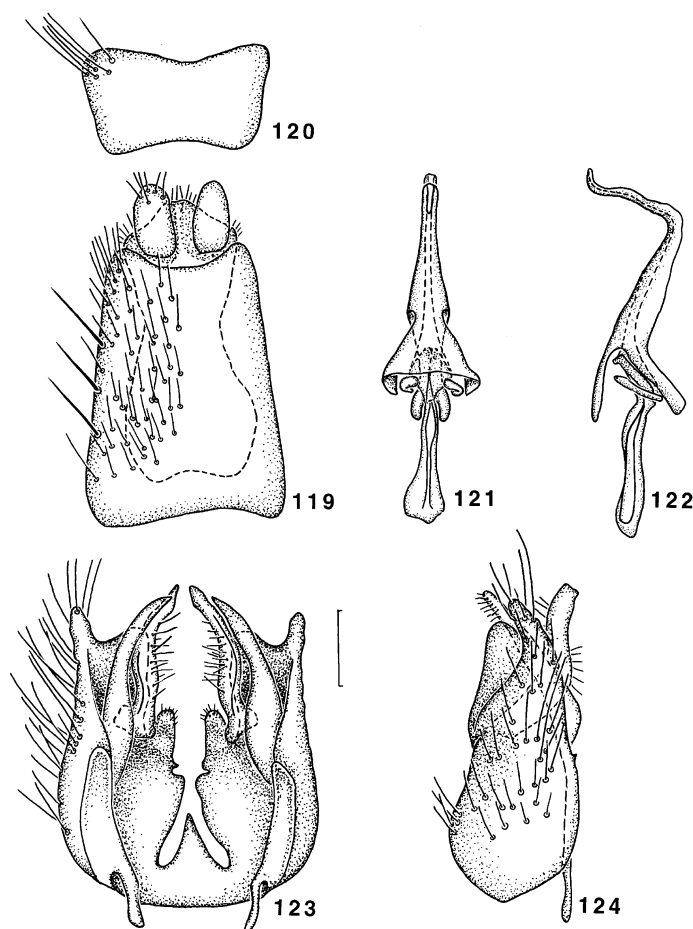
#### *Description*

##### *Male*

Body length: 7–8 mm.

*Head* (Fig. 10). Frons brown, pruinose, brown patch in centre of frons, face silver below this patch; eyes contiguous, facets larger in upper section than those in lower; ocellar tubercle with black, silver pruinescence, several small dark setae; occiput and gena silver pruinose; postocular ridge with single row of black setae; palps small, pale; antennae pale, silver pruinose; scape and pedicel with dark setae, one, sometimes two enlarged setae dorsally on scape; flagellum orange, two to four small setae dorsally at base of first segment, style dark.

*Thorax* (Fig. 25). Scutum and scutellum colouration blue-grey pruinose, patterned with brown, medial stripes and lateral spots; minor setae dark, variable length; pleuron and coxae



**Figs 119–124.** *Nanexila livea* Winterton & Irwin, sp. nov., genitalia (♂): 119, epandrium, dorsal view; 120, tergite 8, dorsal view; 121, aedeagus, dorsal view; 122, same, lateral view; 123, gonocoxites, dorsal view with epandrium and aedeagus removed; 124, same, lateral view. Scale line: 0.2 mm.

grey pruinose; setae on pteropleural callus pale; coxal setae dark; hind coxa two lateral setae; legs pale, distal tarsi segments dark. Scutal chaetotaxy: np 3; sa 1; pa 1; dc 3; sc 1.

**Abdomen (Fig. 25).** Abdomen black; segments 1–5 pale laterally; long pale hairs laterally on segments 1–6; intersegmental membranes pale; terminalia black.

**Genitalia (Figs 119–124).** Epandrium elongate, three to four lateral setae enlarged, width to length ratio: 0.72; tergite 8 broad, slightly constricted medially; gonocoxites separate medially, fused to hypandrium; ventral lobe with apical setae present; gonostylus with medial and ventral setae; inner gonocoxal process narrow, apical setae present ventrally; distiphallus narrow, curved ventrally at almost 90 angle, recurved distally; dorsal apodeme broad, triangular; ventral apodeme forked; *bea* width to length ratio: 0.39.

#### *Female*

Body length: 7–8 mm. Similar to male except:

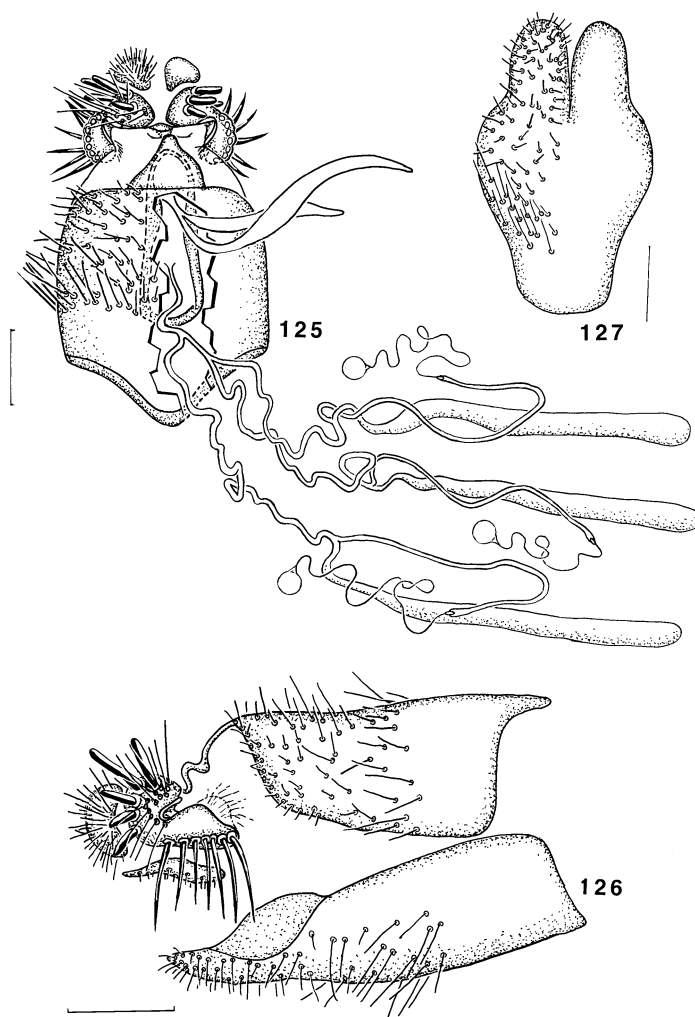
**Head (Fig. 11).** Eyes widely separated by almost twice the width of the ocellar tubercle, eye facets uniform size; frons slightly wrinkled with small black setae; postocular ridge with two rows of setae.

**Abdomen.** Abdomen setae on segments 2–7 small, black; tergite 2 with modified patch of short setae.

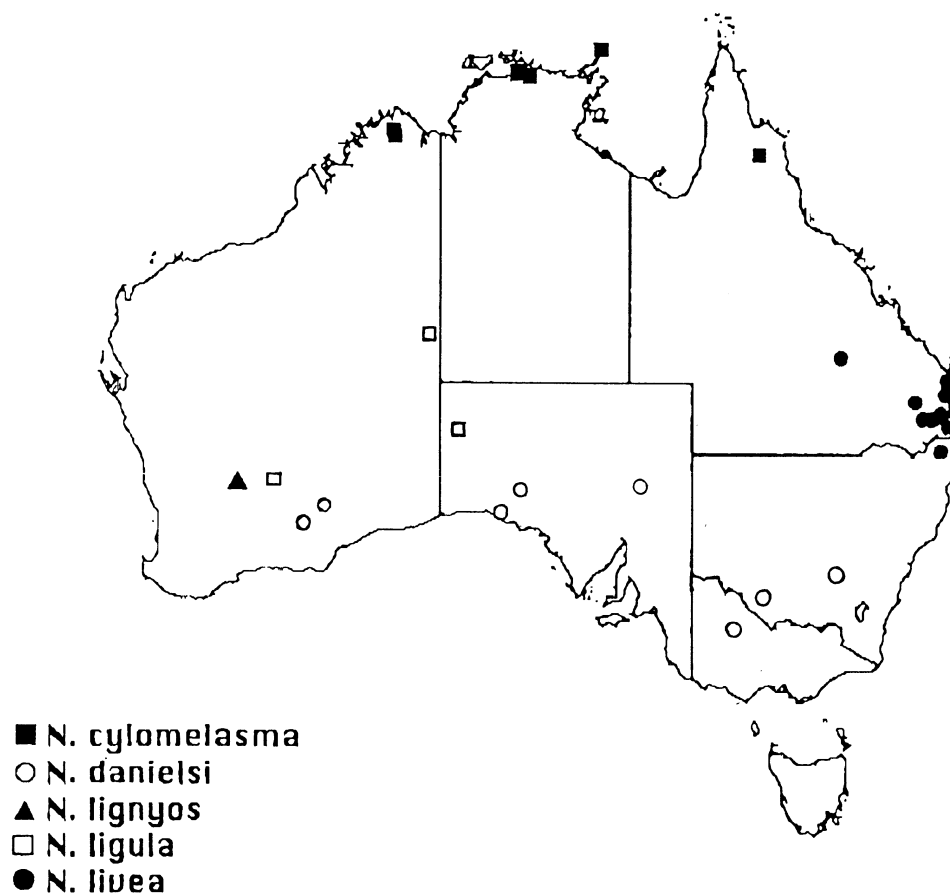
*Genitalia* (Figs 125–127). Furca closed; spermathecal sac trilobate, elongate; ducts long, convoluted, spermathecal ducts joined in pairs to duct of each spermathecal sac lobe; accessory glands symmetrical, unmodified.

#### *Comments*

*Nanexila livea* superficially resembles *N. manni* in body size and scutal patterning, but genitalic differences in both the male and female indicate that the two species are only distantly related, and belong to separate species-groups. The posterior lobe on the outer gonocoxal process and the elongate trilobate spermathecal sac are autapomorphic for the species. *Nanexila livea* is distributed throughout south-eastern Queensland and northern New South Wales (Fig. 128). Males and females sit on tree trunks of *Eucalyptus* species presumably waiting for potential mates. Male *N. livea* were observed on smooth and rough-barked *Eucalyptus* trees approximately 2–4 metres above the ground, where they faced head downwards while slowly lowering and raising their abdomens against the trunk. The specific epithet is from the Latin *liveo*: to turn lead coloured, ashy; referring to the lead-grey coloured scutum.



**Figs 125–127.** *Nanexila livea* Winterton & Irwin, sp. nov., genitalia (♀): 125, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 126, same, lateral view; 127, sternite 8, ventral view. Scale lines: 0.2 mm.



**Fig. 128.** Distribution map for *Nanexila* species; *N. palassa* species-group: *N. cylomelasma*, *N. danielsi*, *N. lignyos*, *N. ligula*, *N. livea*.

*Nanexila palassa* Winterton & Irwin, sp. nov.

(Figs 129–137, 164)

*Material examined*

**Holotype.** ♂, Queensland: 5 km N Leyburn, 27°58'S, 151°38'E, 450 m, 17.ix.1994, G. & A. Daniels, mv lamp, in copula A (MEI#033848) (AM). Condition: good.

**Paratypes.** **Queensland:** ♀, same data as holotype, [in copula with holotype] (MEI#033850) (AM); ♂, ♀, same data as holotype (GDCB) (MEI#033849, 33851); ♂, Lake Broadwater, nr Dalby, site A, 27°21'S, 151°06'E, 27.ix.1986, G. & A. Daniels, mv lamp (MEI#029425) (GDCB); **South Australia:** 3♂, Gammon Ranges Natl Pk, Weetootla Gorge, 30°28'36"S, 139°13'13"E, 11–13.x.1997, S. Winterton, C. Lambkin, J. Skevington, dry creek bed, malaise trap (QM).

*Diagnosis*

Single row of setae on postocular ridge of female; scutum pale with darkened bases of minor setae; male abdomen with bright velutum; epandrium without enlarged posterolateral processes; gonocoxal apodeme reduced; inner gonocoxal process spatulate; abdominal markings absent.

*Description*

*Male*

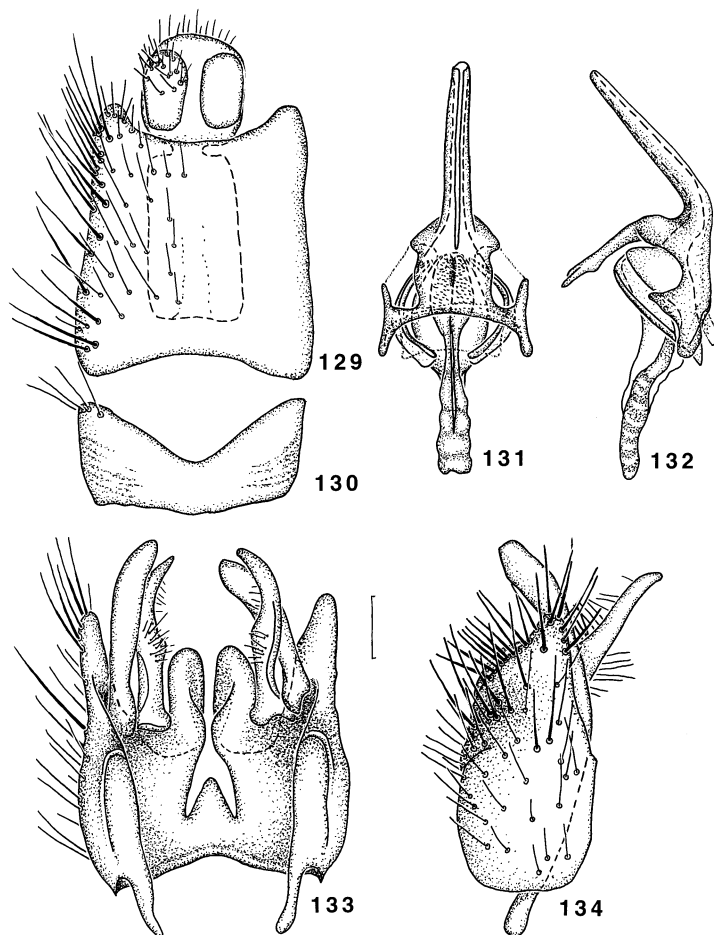
Body length: 6 mm.

**Head.** Frons tan, transverse silver pruinose stripe above antennal bases, brown pruinose patch with several small dark setae above stripe; ocellar tubercle black, silver pruinose; eyes proximate, width at narrowest point slightly greater than width of anterior ocellus; eye facets uniform size; occiput grey pruinose; postocular ridge brown pruinose, single row of dark setae; gena silver pruinose; palp small, pale; scape and pedicel pale yellow, pruinose with small dark setae, usually one, sometimes two enlarged dorsal setae on scape; flagellum orange, 2–3 small dark setae basally; style dark.

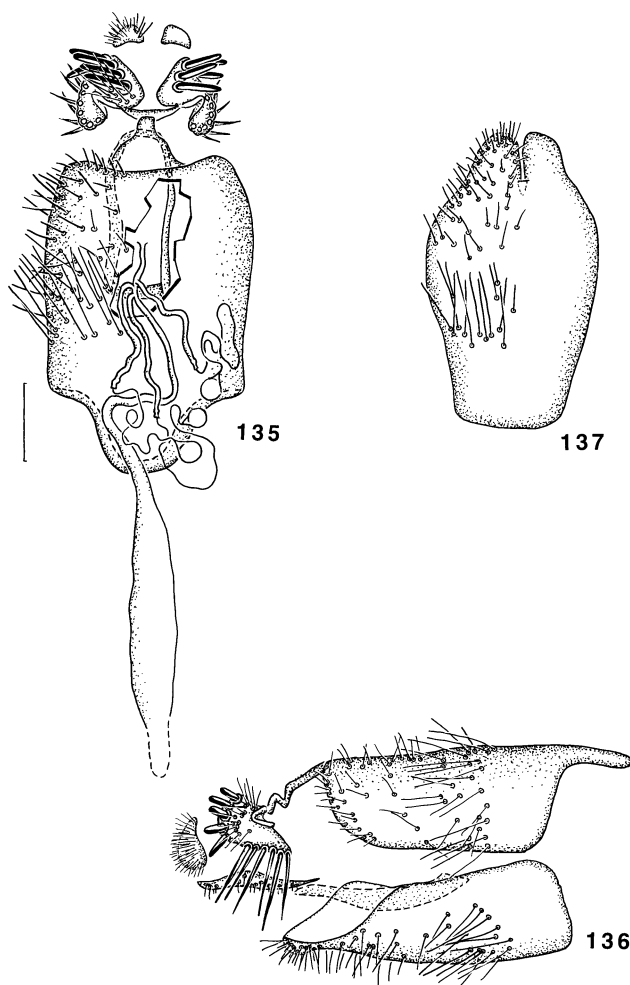
**Thorax.** Thorax grey, pruinose; scutum with small dark setae sparsely distributed, setal bases dark; setae on pteropleural callus pale; legs pale, tarsi darkened distally; coxal setae dark, hind coxa with two lateral setae; wing hyaline, venation dark; haltere pale yellow. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 4; sc 1.

**Abdomen.** Abdomen brown, silver velutum; intersegmental membranes indistinct; long pale hairs laterally on segments 1–6; short dark setae dorsally.

**Genitalia (Figs 129–134).** Epandrium equally as wide as long, enlarged setae laterally, width to length ratio: 1.06; tergite 8 broad, highly constricted medially; gonocoxites separate medially, fused to hypandrium; anterior apodeme reduced; ventral lobe enlarged, glabrous; gonostylus with setae facing medially and ventrally; inner gonocoxal process enlarged,



**Figs 129–134.** *Nanexila palassa* Winterton & Irwin, sp. nov., genitalia (♂): 129, epandrium, dorsal view; 130, tergite 8, dorsal view; 131, aedeagus, dorsal view; 132, same, lateral view; 133, gonocoxites, dorsal view with epandrium and aedeagus removed; 134, same, lateral view. Scale line: 0.2 mm.



**Figs 135–137.** *Nanexila palassa* Winterton & Irwin, sp. nov., genitalia (♀): 135, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 136, same, lateral view; 137, sternite 8, ventral view. Scale line: 0.2 mm.

spatulate; distiphallus long, curved ventrally at base then straight distad; ventral and dorsal apodemes reduced, forked; base of ejaculatory apodeme enlarged, width to length ratio: 0.8, lateral aedeagal process enlarged.

#### *Female*

Body length: 7 mm. Similar to male except:

*Head.* Frons brown pruinose, numerous small dark setae; eyes widely separate, width at narrowest point greater than width of ocellar tubercle; postocular ridge with single row of setae.

*Abdomen.* Abdomen without long pale hairs laterally, segments covered with short dark setae; tergite 2 with modified patch of short setae.

*Genitalia* (Figs 135–137). Furca closed; spermathecal sac simple, elongate, duct short and straight, spermathecal ducts join basally to common spermathecal sac duct.

#### *Comments*

The velutinous pruinose abdomen, pale scutum with dark minor setal bases, enlarged, glabrous ventral lobe and reduced gonocoxal apodemes of the male and the short spermathecal



sac duct of the female, closely relate this species with *N. ruficornis*. *Nanexila palassa* can be distinguished from *N. ruficornis* by the absence of posterolateral processes of the epandrium, spatulate inner gonocoxal processes and a single row of setae on the postocular ridge of the female. *Nanexila palassa* is known from two sites in south-eastern Queensland and from the Gammon Ranges, South Australia (Fig. 164). The specific epithet is derived from the Greek *palassa*: sprinkle, spot, bespatter; pertaining to the dark setal bases on the scutum which appear as a sprinkle of dark spots.

*Nanexila spilotis* Winterton & Irwin, sp. nov.

(Figs 26, 138–146, 164)

*Material examined*

*Holotype*. ♂, Western Australia: Deep Reach Pool, Millstream, Chichester Natl Pk, 21°37'S, 117°06'E, 22.viii.1996, J. O'Grady, at light (MEI#090733) (WAM). Condition: good.

*Paratypes*. **South Australia**: 4♀, Gammon Ranges Natl Pk, Weetootla Gorge, 30°28'36"S, 139°13'13"E, 11–13.x.1997, S. Winterton, C. Lambkin, J. Skevington, dry creek bed, malaise trap (QM); 2♀, Flinders Ranges Natl Pk, Love Range Mine Rd, 31°24'06"S, 138°46'53"E; 8–10.x.1997, S. Winterton, J. & A. Skevington, C. Lambkin, malaise trap in *Callitris* and mallee lined creek bed (UQIC); ♂, ♀, Blanchetown, N.B. Tindale (SAM); ♀, 35 miles E Ceduna, 28.xi.1958, E.F. Riek (MEI#029416) (ANIC); ♀, Great Victoria Desert, Eastern side Serpentine Lakes, 28°30'S, 129°01'E, 26.viii. 1980, J. Forrest, at light nr *Euc.[alyptus]* on dunes (SAM); **Western Australia**: ♂, 2♀, same data as holotype (MEI#090734–6) (WAM); **Northern Territory**: ♂, 53 km NE Alice Springs, 6.x.1978, D.H. Colless, at light (MEI#029418) (ANIC).

*Diagnosis*

Abdominal markings present; epandrium with dense enlarged setae along lateral edge; enlarged gonocoxal apodemes; inner gonocoxal process spatulate; subepandrial sclerite simple.

*Description*

*Male*

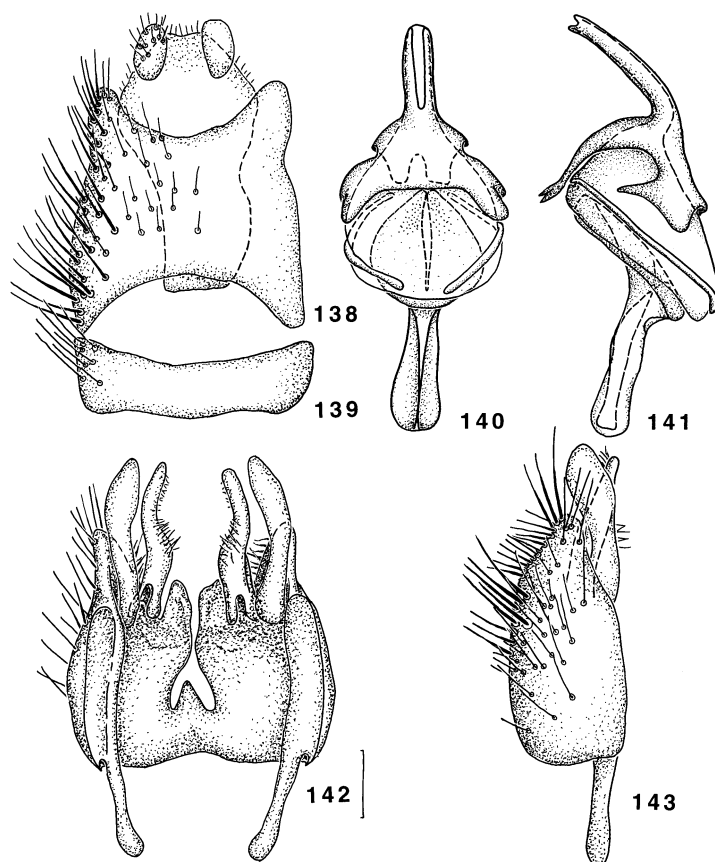
Body length: 6 mm.

*Head*. Frons tan, silver pruinose, brown patch above antennal bases, two to three small dark setae above patch; ocellar tubercle black, silver pruinose; eyes proximate, width at narrowest point slightly less than width of anterior ocellus; eye facets larger in upper section than in lower; occiput light brown-grey pruinose; postocular ridge with single row of dark setae; gena silver pruinose; palp small, pale; antennae silver pruinose; scape and pedicel pale yellow with small dark setae, usually one, sometimes two dorsal setae on scape enlarged twice the size of other setae; flagellum orange with 2–3 small dark setae basally; distal segments dark.

*Thorax*. Scutum and scutellum brown or grey, silver pruinose, small dark setae sparsely distributed, setal bases dark; pleuron grey pruinose; setae on pteropleural callus pale; legs pale, tarsi darkened distally; coxal setae dark, hind coxa with two lateral setae; wing hyaline, venation pale basally, dark distally; haltere pale yellow. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 3–4; sc 1.

*Abdomen*. Abdomen pale yellow; intersegmental membranes white; long pale hairs laterally on segments 1–7; dark medial spot on segments 1–6, short dark setae dorsally.

*Genitalia* (Figs 138–143). Epandrium broad, wider than long, emarginate anteriorly and posteriorly, enlarged setae laterally, width to length ratio: 1.59; tergite 8 short, medially hardly constricted; gonocoxites separate medially, fused to hypandrium; anterior apodeme enlarged; ventral lobe glabrous; gonostylus with setae facing medially and ventrally; inner gonocoxal process enlarged, spatulate; distiphallus curved ventrally; ventral and dorsal apodemes reduced, forked; base of ejaculatory apodeme enlarged, width to length ratio: 0.86, lateral aedeagal process enlarged.



**Figs 138–143.** *Nanexila spilotis* Winterton & Irwin, sp. nov., genitalia (♂): 138, epandrium, dorsal view; 139, tergite 8, dorsal view; 140, aedeagus, dorsal view; 141, same, lateral view; 142, gonocoxites, dorsal view with epandrium and aedeagus removed; 143, same, lateral view. Scale line: 0.2 mm.

#### Female

Body length: 7 mm. Similar to male except:

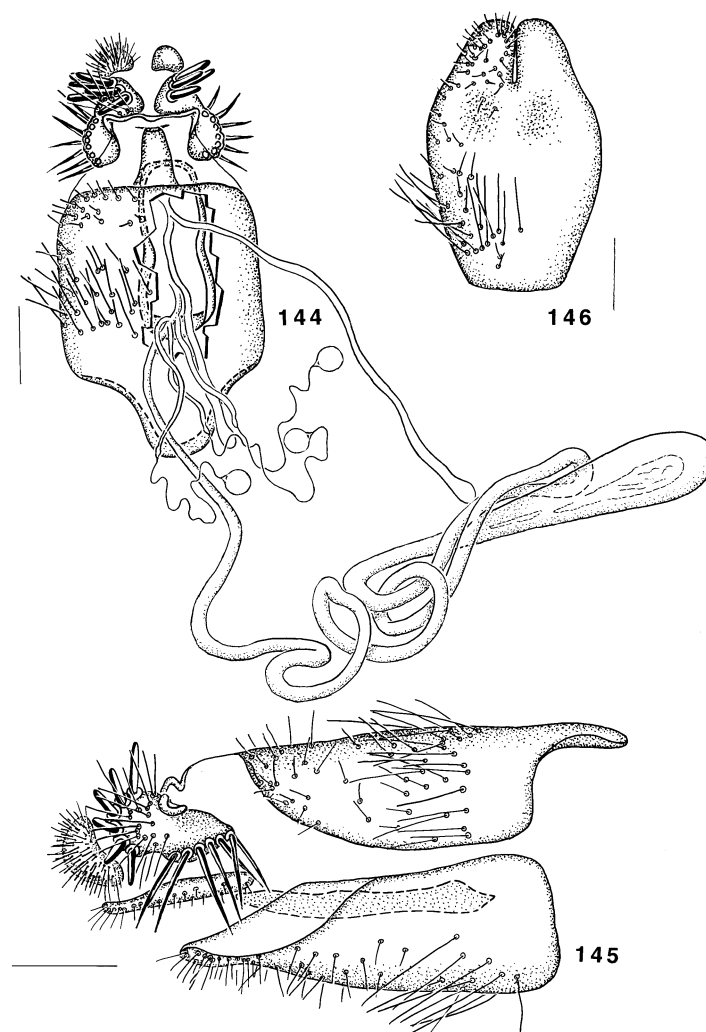
**Head.** Frons brown pruinose, small dark setae sparsely distributed; eyes widely separate, width at narrowest point much greater than width of ocellar tubercle; eye facets uniform size; postocular ridge with two irregular rows of dark setae; flagellum brown.

**Abdomen** (Fig. 26). Abdomen without long pale hairs laterally, segments covered with short dark setae; tergite 2 with modified patch of short setae.

**Genitalia** (Figs 144–146). Furca closed; spermathecal sac simple, elongate, duct long and convoluted, spermathecal ducts join basally to common spermathecal sac duct; accessory glands asymmetrical.

#### Comments

*Nanexila spilotis* forms a distinct subgroup (clade 21) with *N. danielsi* and *N. ligula* (Fig. 184), all of which have enlarged, spatulate inner gonocoxal processes and enlarged gonocoxal apodemes (the male of *N. lignyos* is unknown). *Nanexila spilotis* is easily identified by the presence of abdominal markings and a pale scutum with darkened minor setae bases (Fig. 26). The species has been collected from coastal Western and South Australia, and from central Australia (Fig. 164). The specific epithet is derived from the Greek *spilos*: spot, stain; pertaining to the abdominal markings.



**Figs 144–146.** *Nanexila spilotis* Winterton & Irwin, sp. nov., genitalia (♀): 144, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 145, same, lateral view; 146, sternite 8, ventral view. Scale lines: 0.2 mm.

***Nanexila variabilis* Winterton & Irwin, sp. nov.**

(Figs 6, 7, 147–154, 164)

*Material examined*

*Holotype.* ♂, Western Australia: Pingrup, 21.xi.1958, E.F. Riek (MEI#028722) (ANIC). Condition: good.

*Paratypes.* **Western Australia:** 2♂, same data as holotype (MEI#028720, 28726) (ANIC); ♂, 40 miles E Balladonia, 21.iii.1968, I.F.B. Common & M.S. Upton (MEI#028723) (ANIC); ♂, 50 miles S Coolgardie, 28.x.1958, E.F. Riek (MEI#028724) (ANIC); **Northern Territory:** 3♂, 2♀, 53 km NE Alice Springs, 6.x.1978, D.H. Colless, at light (MEI#028719, 28730–33) (ANIC); **South Australia:** 3♂, 40 miles E Nullarbor, 18.iii.1968, I.F.B. Common & M.S. Upton (MEI#028725, 28727, 28729) (ANIC); ♂, Poochera, 22.x.1977, D. H. Colless, at light (MEI#028734) (ANIC); **Queensland:** ♂, Killarney, 1.xi.1961, I.F.B. Common & M.S. Upton (MEI#028726) (ANIC); **New South Wales:** ♂, 23 km SSE Byrock, 30°50'S, 146°33'E, 20.x.1975, M.S. Upton (MEI#028728) (ANIC).

*Diagnosis*

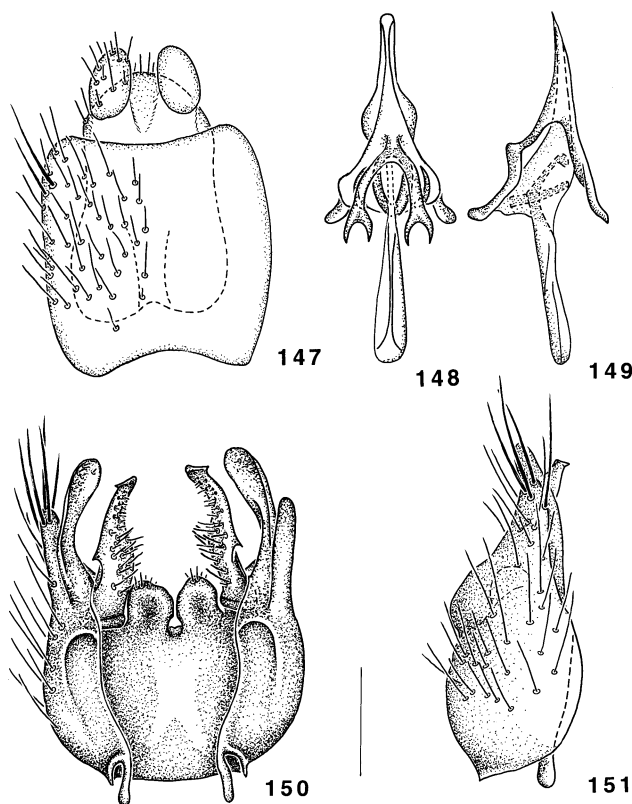
Abdomen pale; aedeagus with arms of ventral apodeme secondarily forked; quadrate epandrium; enlarged seta on epandrium; spermathecal sac simple.

*Description**Male*

Body length: 5–6 mm.

*Head* (Fig. 6). Frons tan, brown patch above antennal bases, silver pruinose below this patch; ocellar tubercle black, silver pruinose; eyes contiguous; eye facets only slightly larger in upper section than in lower; occiput grey pruinose; postocular ridge with single row of dark setae; gena silver pruinose; palp small, pale; scape and pedicel pale yellow, pruinose with small dark setae, two or three dorsal setae on scape enlarged; flagellum brown or orange, 2–3 small dark setae basally; style dark.

*Thorax*. Scutum and scutellum grey, pruinose, small dark setae sparsely distributed over scutum, length variable; scutal macrosetae dark or pale; pleuron grey, pruinose; setae on pteropleural callus pale; legs pale, tarsi slightly darkened distally; forecoxa pale yellow, mid and hind coxae grey, pruinose; coxal setae pale or dark, hind coxa with two, occasionally one lateral setae; wing hyaline, venation pale; haltere pale yellow. Scutal chaetotaxy: np 3; sa 1; pa 1; dc 3–4; sc 1.



**Figs 147–151.** *Nanexila variabilis* Winterton & Irwin, sp. nov., genitalia (♂): 147, epandrium, dorsal view; 148, aedeagus, ventral view; 149, same, lateral view; 150, gonocoxites, dorsal view with epandrium and aedeagus removed; 151, same, lateral view. Scale line: 0.2 mm.

*Abdomen.* Abdomen pale yellow, sometimes darkened medially to an extent that whole tergite is dark; intersegmental membranes white; long pale hairs laterally on segments 1–7; short, dark setae dorsally.

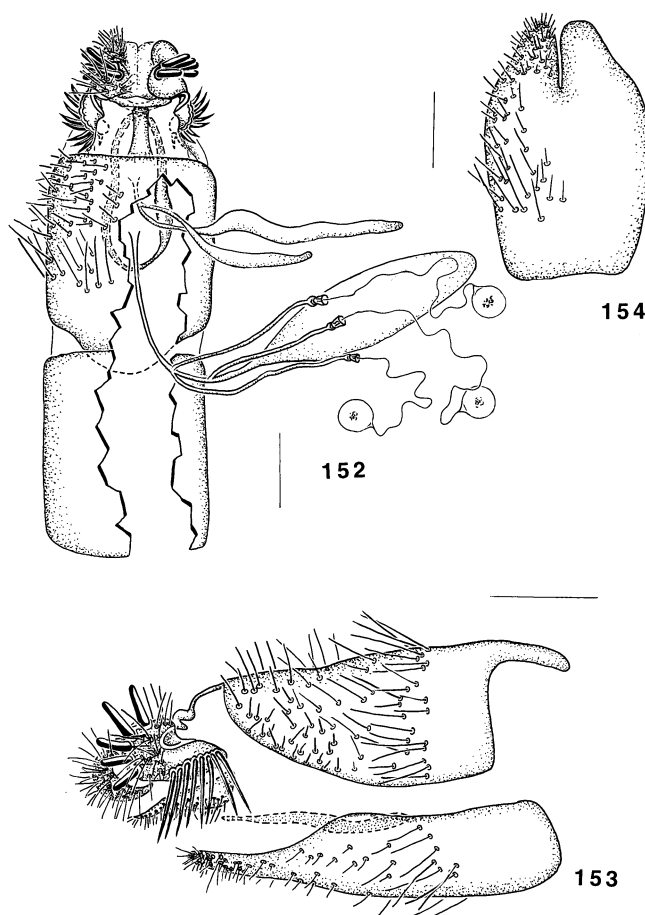
*Genitalia (Figs 147–151).* Epandrium broad, quadrangular, width equal to length along midline, slightly emarginate anteriorly, enlarged seta on posterolateral corner, width to length ratio: 0.88; gonocoxites fused medially; hypandrium completely fused to gonocoxites, indistinct; ventral lobe small, circular, apical setae present; gonostylus sclerotised apically, setae facing medially and ventrally; inner gonocoxal process enlarged, spatulate; distiphallus short, straight; ventral and dorsal apodemes reduced, forked, ventral apodeme secondarily forked; *bea* width to length: 0.46.

#### *Female*

Body length: 5–6 mm. Similar to male except:

*Head (Fig. 7).* Frons grey pruinose, numerous small dark setae sparsely distributed; eyes widely separate, distance at narrowest point almost twice width of ocellar tubercle; eye facets uniform size; postocular ridge with two irregular rows of pale setae.

*Abdomen.* Abdomen without long pale hairs laterally, segments covered with short dark setae; tergite 2 with medial patch of very short setae.



**Figs 152–154.** *Nanexila variabilis* Winterton & Irwin, sp. nov., genitalia (♀): 152, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 153, same, lateral view; 154, sternite 8, ventral view. Scale lines: 0.2 mm.

*Genitalia* (Figs 152–154). Furca closed; spermathecal sac simple, elongate, duct short and straight, spermathecal ducts join basally to common spermathecal sac duct; accessory glands symmetrical.

#### Comments

The scutal colouration and abdominal markings are highly variable in this species. The abdominal tergites are commonly pale yellow with brown markings, but in some individuals the abdomen is unmarked, while in others the abdominal markings cover so much of the tergite that the abdominal colouration appears dark. The secondary forking of the ventral apodeme of the male aedeagus is autapomorphic. *Nanexila variabilis* is distributed throughout southern Australia and north into south-eastern Queensland (Fig. 164). The specific epithet is derived from the Latin *variabilis*: changeable; referring to the variable colouration and markings.

### *Nanexila vittata* Winterton & Irwin, sp. nov.

(Figs 1, 12, 13, 17c,d, 19, 27, 155–160, 164)

#### Material examined

*Holotype*. ♂, Queensland: Carnarvon Natl Pk, Mt Moffatt Section, West branch, Maranoa River, (site 16), 25°08'22"S, 147°50'37"E, 660 m amsl, 26.xi.1995, M.E. Irwin, S.D. Gaimari, ex. 9 m Focks malaise trap (MEI#031613) (QM). Condition: good.

*Paratypes*. **Queensland**: 7♂, ♀, same data as holotype (MEI#031219, 31595, 31581–3, 31606–7, 31629) (QM); 7♂, Carnarvon Natl Pk, Mt Moffatt Section, 3 km SE park headquarters, 25°04'39"S, 148°00'30"E, 740 m amsl, 20.xi.1995, M.E. Irwin, sand under *Eucalyptus* tree [reared from larva; pupal case mounted beneath specimen] (MEI#049553) (QM); ♀, Carnarvon Natl Pk, Mt Moffatt Section (site 17), 25°04'39"S, 148°00'30"E, 740 m amsl, 24.xi.1995, M.E. Irwin, S.D. Gaimari, ex. 9 m Focks malaise trap (MEI#030884) (QM); ♀, Carnarvon Natl Pk, Mt Moffatt Section, base of the Tombs (site 15), 25°04'54"S, 147°52'32"E, 700 m amsl, 24.xi.1995, M.E. Irwin, S.D. Gaimari, ex. 9 m Focks malaise trap (MEI#031413) (QM); ♂, 3♀, Carnarvon Natl Pk, Mt Moffatt Section, Kenniffs Cave (site 23), 24°52'26"S, 148°01'19"E, 840 m amsl, 24.xi.1995, M.E. Irwin, S.D. Gaimari, ex. 9 m Focks malaise trap (MEI#030889, 31306–8) (ANIC); 2♂, 6♀, Carnarvon Natl Pk, Marlong Ck, nr Lots Wife (site 13), 24°58'08"S, 147°57'13"E, 760 m amsl, 25.xi.1995, M.E. Irwin, S.D. Gaimari, ex. 9 m Focks malaise trap (MEI#031266, 31381, 31452, 31460, 31462, 31473, 31467) (ANIC); ♂, ♀, 6 km N Taroom, 25°36'S, 149°46'E, 26.xi.1992, 200 m, G. Daniels, mv lamp (MEI#033674–5) (GDCB).

#### Diagnosis

Transverse pruinose band across frons; brown, longitudinal, thoracic stripes; scutum with pruinose quadrate, without two arms projecting anteriorly; trilobate spermathecal sac; female with elongate abdominal markings

#### Description

Similar to *N. argentiquadris* except:

##### Male

Body length: 6–8 mm.

*Head* (Fig. 12). Pale brown band across frons.

*Thorax* (Figs 19, 27). Scutum orange-pink, gold pruinose, two brown, longitudinal stripes, dark quadrate patch located posteromedially between dorsocentral setae, gold pruinose; notopleural setae pale, setae on pteropleural callus pale; legs wholly yellow; setae on fore and mid coxae pale; hind coxa with one lateral seta; wing hyaline, venation mostly dark. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 3 (anterior seta minute); sc 1.

*Abdomen*. Tergites without markings.

*Genitalia* (Figs 155–160). Epandrium width to length ratio: 0.81; gonocoxites separate medially, fused to hypandrium; ventral lobe glabrous; distiphallus straight; *bea* width to length ratio: 0.39.

#### *Female*

Body length: 8–9 mm.

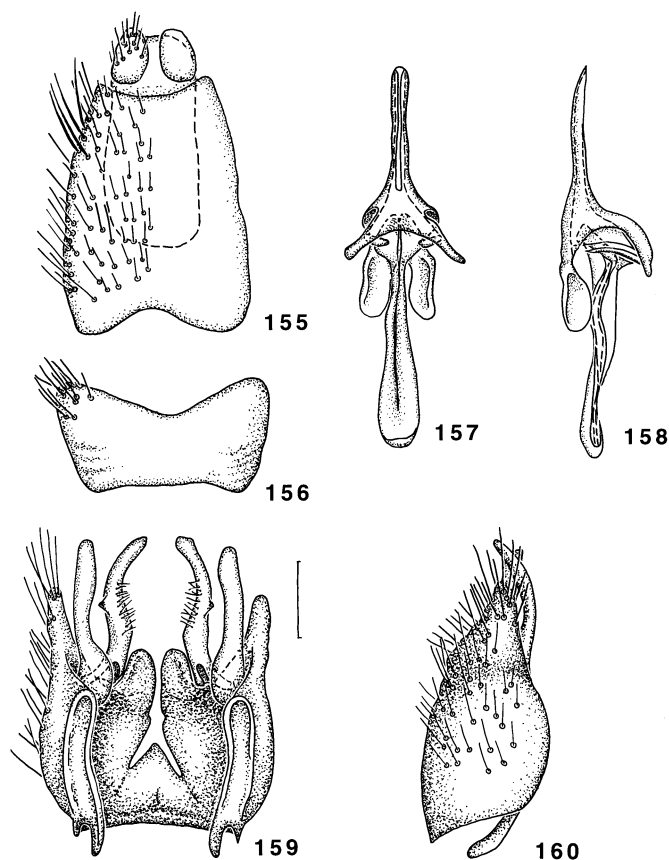
*Head* (Fig. 13). Prominent transverse band across frons

*Abdomen* (Figs 17, 27). Medial abdominal markings on tergites 3–7, elongate; well-developed patch of modified setae posteromedially on tergite 2.

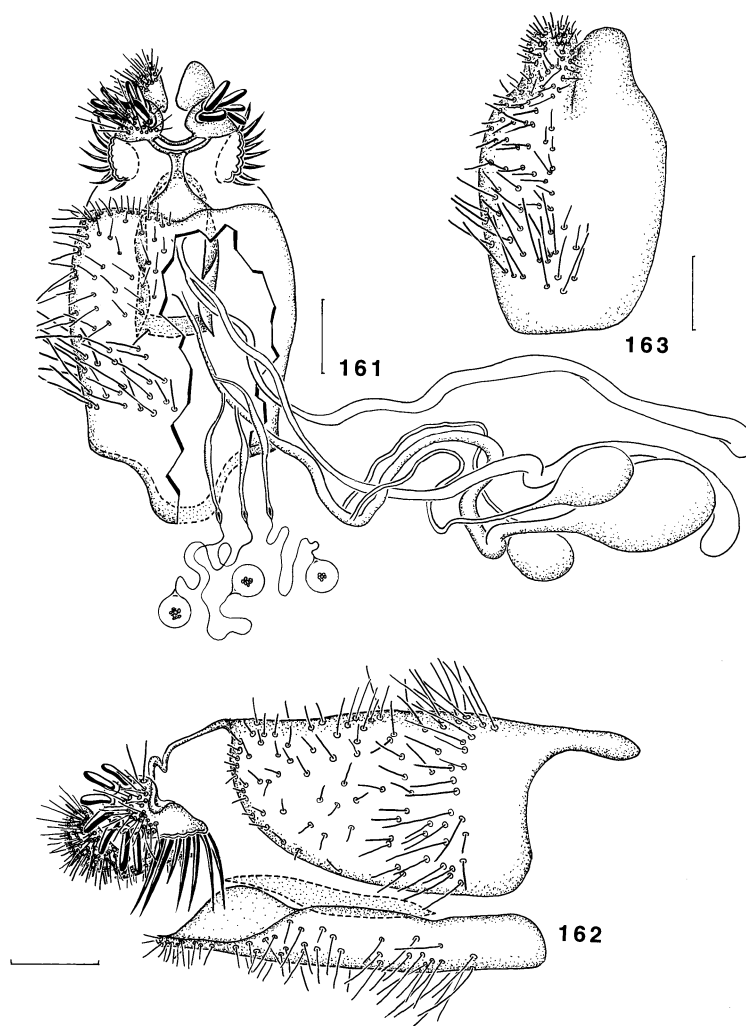
*Genitalia* (Figs 161–163). Furca closed; spermathecal sac trilobate, single median sac with two smaller lateral sacs, spermathecal ducts join basally to common spermathecal sac duct; accessory glands simple, elongate, length equal to that of spermathecal sac, symmetrical.

#### *Comments*

*Nanexila vittata* is closely related to *N. argentiquadris* based on the presence of trilobate spermathecal sac arrangement, four notopleural setae and two supra-alar setae. The ‘paddle’-shaped arms of the ventral apodeme and the pruinose scutal quadrate link these two species with *N. cylomelasma* (clade 17). All specimens of *N. vittata* have been collected from central Queensland (fig. 164). The abdominal markings and the facial band are sexually dimorphic,



**Figs 155–160.** *Nanexila vittata* Winterton & Irwin, sp. nov., genitalia (♂): 155, epandrium, dorsal view; 156, tergite 8, dorsal view; 157, aedeagus, dorsal view; 158, same, lateral view; 159, gonocoxites, dorsal view with epandrium and aedeagus removed; 160, same, lateral view. Scale line: 0.2 mm.



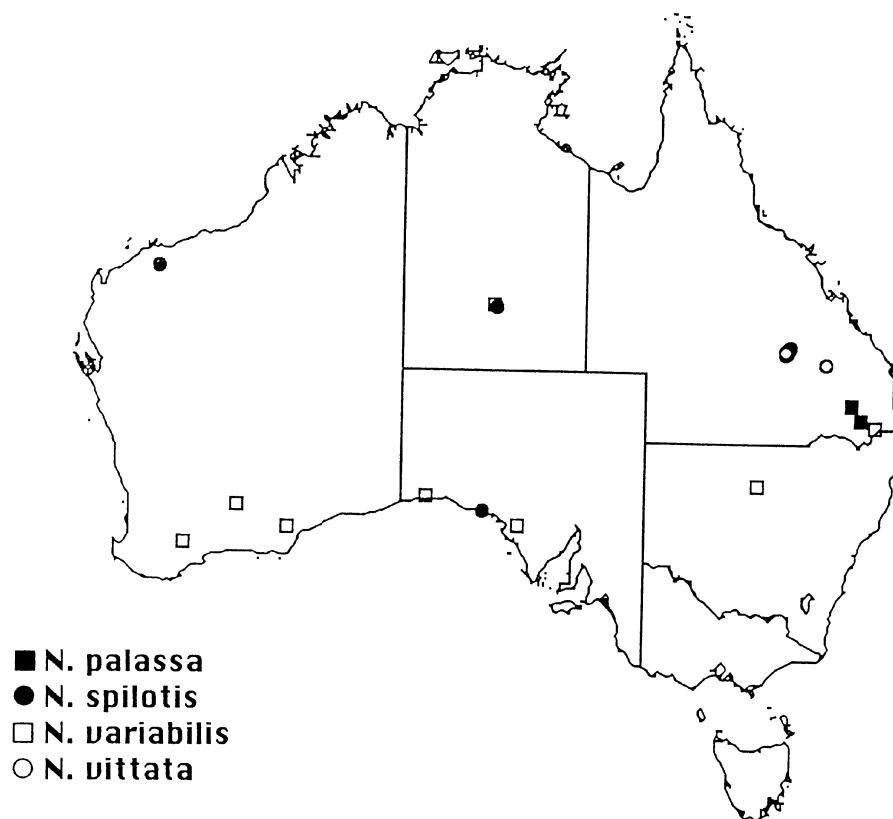
**Figs 161–163.** *Nanexila vittata* Winterton & Irwin, sp. nov., genitalia (♀): 161, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 162, same, lateral view; 163, sternite 8, ventral view. Scale lines: 0.2 mm.

being well developed in the female and are more elongate than those present in *N. argentiquadris*. The modified patch of setae on female tergite 2 is best developed in this species. The specific epithet is derived from the Latin *vitta*: ribbon, striped; referring to the longitudinal stripes on the thorax.

#### ***Nanexila atricostalis* species-group**

This species-group (clade 6) consists of four closely related species characterised by: female abdomen with velutum; numerous enlarged setae on the scape and pedicel; trilobate spermathecal sac arrangement. All species in this group are distinctive and may eventually be found to represent a genus separate from *Nanexila*. The male is unknown for *N. aureilineata*, *N. intermedia* and *N. paradoxa*. The relationships of the species in this group to the rest of the genus will become clearer once more males are examined.





**Fig. 164.** Distribution map for *Nanexila* species; *N. palassa* species-group: *N. palassa*, *N. spilotis*, *N. variabilis*, *N. vittata*.

*Nanexila atricostalis* Winterton & Irwin, sp. nov.

(Figs 14, 15, 20, 28, 165–173, 183)

*Material examined*

*Holotype.* ♂, Queensland: 6 km N Bell, 9.iv.1957, E.F. Riek (MEI#028766) (ANIC). Condition: good

*Paratypes.* **Queensland:** ♀, same data as holotype (MEI#028767) (ANIC); 3 ♀, Scrub Rd, Brisbane Forest Pk, 27°25'05"S, 152°50'13"E, 17.x.–26.xi.1997, S. Winterton, N. Power, D. White, malaise trap, open *Eucalyptus* forest (QM).

*Diagnosis*

Enlarged setae on scape and pedicel; scutum colour silver-green pruinose; abdominal pattern as in figure 28; trilobate spermathecal sac arrangement, sacs small, globose, spermathecal ducts joined in pairs to duct of each spermathecal sac lobe; pteropleural callus setae dark.

*Description*

*Male*

Body length: 6 mm.

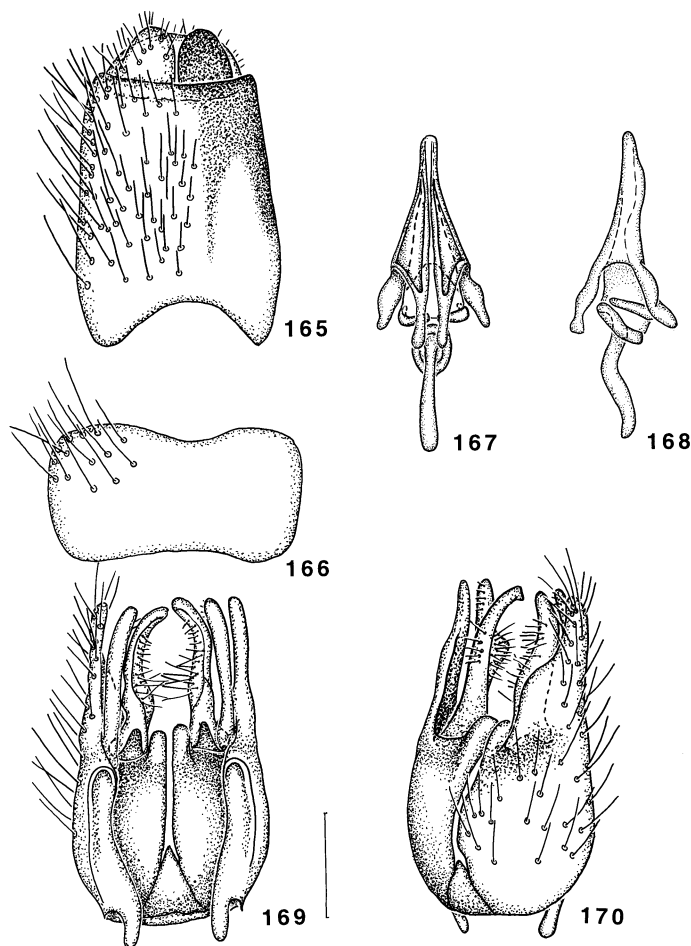
*Head* (Fig. 14). Frons gold pruinose, patches of four dark setae over tentorial pits; eyes proximate, not contiguous; facets uniform size throughout; ocellar tubercle gold pruinose, dark setae projecting anterodorsally; occiput silver-green pruinose; postocular ridge with single row of setae; gena silver pruinose with numerous long black hairs; palp reduced, pale; scape and

pedicel pale, silver pruinose with numerous large, black setae; flagellum orange, basal segment with two small black setae dorsolaterally; style darkened.

**Thorax (Fig. 20, 28).** Scutum and scutellum silver-green pruinose; scutum with numerous dark setae about half the length of macrosetae; hairs on pteropleural callus predominantly dark; fore and middle coxae with numerous dark setae; hind coxa with two dark lateral setae; large setae on all coxa interspersed with smaller, dark setae; femora dark, with numerous dark setae of two different lengths; tibia and tarsi pale; wing with distinctive infuscation of costal area, venation dark; haltere knob dark, stem pale. Scutal chaetotaxy: np 3; sa 1; pa 1; dc 4; sc 1.

**Abdomen (Fig. 28).** Abdomen patterned; intersegmental membranes pale; segments with faint gold velutum, long pale hairs laterally; tergites with short and dark setae medially.

**Genitalia (Figs 165–170).** Epandrium slightly elongate, emarginate anteriorly, patterned as in figure 165, width to length ratio: 0.88; tergite 8 relatively long, slightly constricted medially; gonocoxites separate, hypandrium separate from gonocoxites; ventral lobe small; gonostylus with dorsal process (Fig. 170), setae projecting ventrally and medially; aedeagal complex relatively small; distiphallus straight; dorsal and ventral apodemes forked, reduced; *bea* width to length ratio: 0.64.



**Figs 165–170.** *Nanexila atricostalis* Winterton & Irwin, sp. nov., genitalia (♂): 165, epandrium, dorsal view; 166, tergite 8, dorsal view; 167, aedeagus, ventral view; 168, same, lateral view; 169, gonocoxites, dorsal view with epandrium and aedeagus removed; 170, same, lateroventral view. Scale line: 0.2 mm.

*Female*

Body length: 8 mm. Similar to male except:

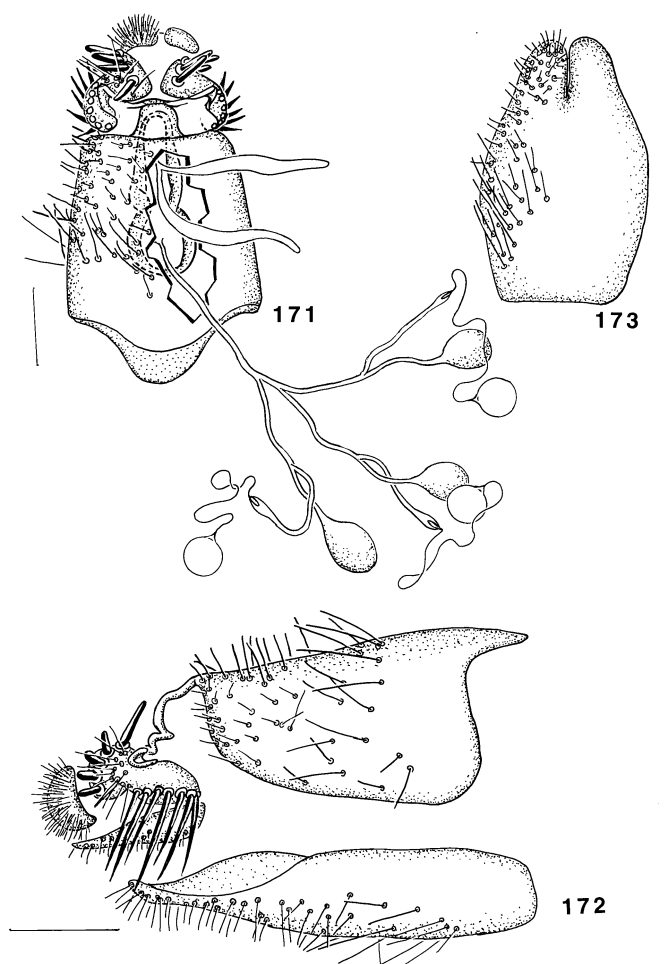
*Head (Figs 15).* Frons wider than ocellar tubercle; two rows of setae on postocular ridge, many setae pale.

*Thorax and abdomen.* All minor setae on scutum small, less than quarter of length of macrosetae; femora pale, all setae small; abdominal segments with small dark setae, lacking long pale hairs laterally.

*Genitalia (Figs 171–173).* Furca closed, constricted approximately midway; reproductive system trilobate, three sacs with separate ducts leading to a common duct, spermathecal ducts joined in pairs to duct of each spermathecal sac lobe; spermathecal sacs small, slightly larger than spermathecae.

*Comments*

Sexual dimorphism is particularly evident in *N. atricostalis*. Sexes may be differentiated by colouration of the femora, proximity of the eyes and presence of longer minor setae on the scutum in the male. Both sexes have faint golden velutum on the abdomen. The specific epithet



**Figs 171–173.** *Nanexila atricostalis* Winterton & Irwin, sp. nov., genitalia (♀): 171, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 172, same, lateral view; 173, sternite 8, ventral view. Scale lines: 0.2 mm.

is derived from the Latin *ater*: black; *costa*: rib; referring to the darkened costal area of the wing. *Nanexila atricostalis* is recorded from Bell, south-eastern Queensland (Fig. 183).

*Nanexila aureilineata* Winterton & Irwin, sp. nov.

(Figs 21, 29, 174–176, 183)

*Material examined*

*Holotype*. ♀, Queensland: Windsor Tableland via Mt Carbine, N Qld, 10.xi–26.xii.1983, Storey & Titmarsh, malaise trap (MEI#090737) (QM). Condition: good.

*Paratypes*. **Queensland**: ♀, same data as holotype (MEI#090738) (QM); ♀, 16 km up Davies Ck Rd via Mareeba, N Qld, 2.xii.1984–7.i.1985, Storey & Titmarsh (MEI#090739) (QDPI); ♀, Mt Lewis, N Qld, 30.x.–13.xi.1980, R.I. Storey, malaise trap (MEI#090740) (QDPI); ♀, Mt Lewis, N Qld, 16–29.x.1980, R.I. Storey, malaise trap (MEI#090741) (QDPI).

*Diagnosis*

Enlarged setae on scape and pedicel; scutum dark brown with gold pruinose stripe; female abdomen black with silver and gold velutum; trilobate spermathecal sac arrangement; sacs larger than spermathecae, spermathecal ducts joined in pairs to duct of each spermathecal sac lobe.

*Description*

*Female*

Body length: 8–11 mm.

*Head*. Frons gold pruinose, dark median line, very small, sparse setae, tentorial pits darkened; distance between eyes equal to width of ocellar tubercle; ocellar tubercle gold pruinose with small dark setae; eye facets uniform size throughout; occiput bright golden pruinose; postocular ridge with single row of dark setae; gena silver pruinose; palp enlarged with numerous long dark hairs; scape and pedicel gold pruinose with long dark setae, setae at distal end of scape larger than rest; flagellum brown-gold pruinose, patch of small dark setae located towards base of first segment; style dark.

*Thorax* (Fig. 21, 29). Scutum and scutellum dark brown pruinose, vivid gold pruinose stripe medially; small dark setae sparsely distributed over scutum; pleuron and coxae dark brown-silver pruinose; setae on pteropleural callus predominantly dark; coxal setae dark; hind coxa with two pairs of lateral setae; colouration of femora variable, sometimes hind- and mid-coxa dark brown, otherwise all coxae, tibia and tarsi pale yellow; wing infusate, particularly costal and radial areas (Fig. 21); haltere knob dark, stem pale. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 3; sc 1.

*Abdomen* (Fig. 29). Abdomen dark brown-black; segments 1–5 with silver pruinescence posterolaterally; intersegmental membranes dark; setae on segment 1 long and thin, pale; setae on rest of segments small and dark.

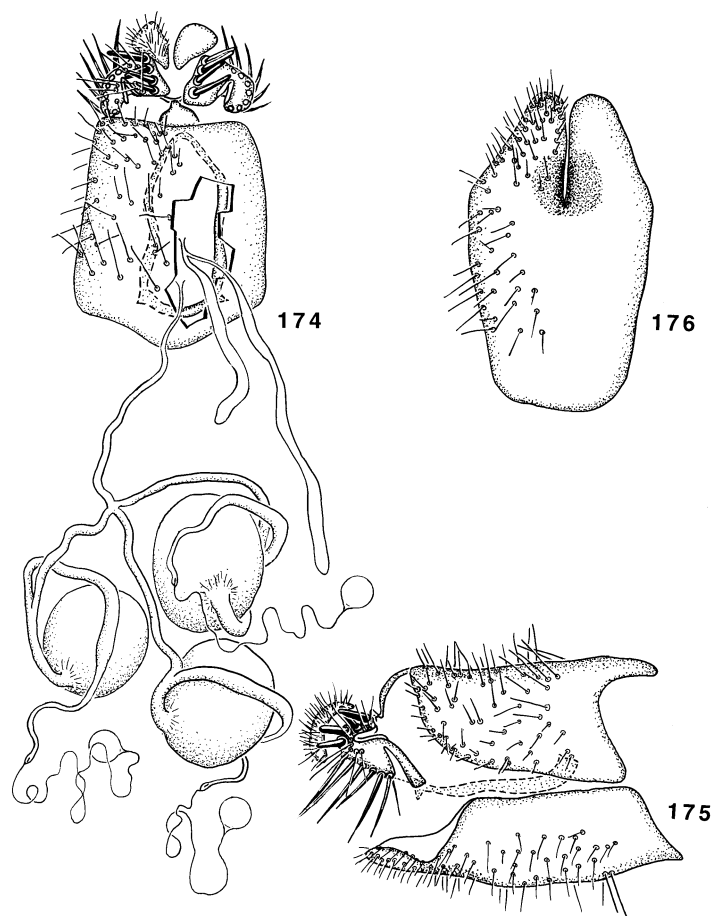
*Genitalia* (Figs 174–176). Furca closed, with posterolateral processes; reproductive system trilobate, spermathecal sacs larger than spermathecae, spermathecal ducts thickened, muscular, spermathecal ducts joined in pairs to duct of each spermathecal sac lobe; accessory glands asymmetrical.

*Male*

Unknown.

*Comments*

The infusate wings and gold pruinose stripe on the scutum make this species easily recognisable. *Nanexila aureilineata* is known only from far northern Queensland (Fig. 183). The specific epithet is derived from the Latin *auratus*: ornamented with gold; *lineata*: of a line; referring to the gold stripe on the scutum.



**Figs 174–176.** *Nanexila aureilineata* Winterton & Irwin, sp. nov., genitalia (♀): 174, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 175, same, lateral view; 176, sternite 8, ventral view.

*Nanexila intermedia* Winterton & Irwin, sp. nov.

(Figs 177–179, 183)

*Material examined*

*Holotype.* ♀, New South Wales: Thredbo, 10.i.1988, E. Baker (MEI#090742) (ANIC). Condition: good, abdomen in genitalia vial on pin beneath specimen.

*Diagnosis*

Scutum uniform yellow-brown; spermathecal sac trilobate, spermathecal ducts joined alternately to common spermathecal sac duct; postocular ridge with anterior row of setae dark, posterior row pale.

*Description*

*Female*

Body length: 8 mm.

*Head.* Frons and occiput brown, gold pruinose; eyes separate, distance approximately twice width of ocellar tubercle; frons wrinkled, several small dark setae; postocular ridge with

two rows of setae, anterior row black, posterior row pale; gena grey pruinose; palp small, pale; antennae brown, gold pruinose; scape and pedicel with dark setae, scape with most setae enlarged; flagellum orange, setae absent; style dark.

*Thorax.* Scutum pale brown, gold pruinose, patterned with darker brown; small dark setae sparsely covering scutum, length variable; pleuron and coxae grey pruinose; setae on pteropleural callus dark; hind coxa with two lateral setae; legs pale, terminal tarsi segment dark. Scutal chaetotaxy: np 3; sa 1 on left side and 2 on right; pa 1; dc 4; sc 1.

*Abdomen.* Abdomen dark brown, venter grey; intersegmental membranes pale; terminalia brown.

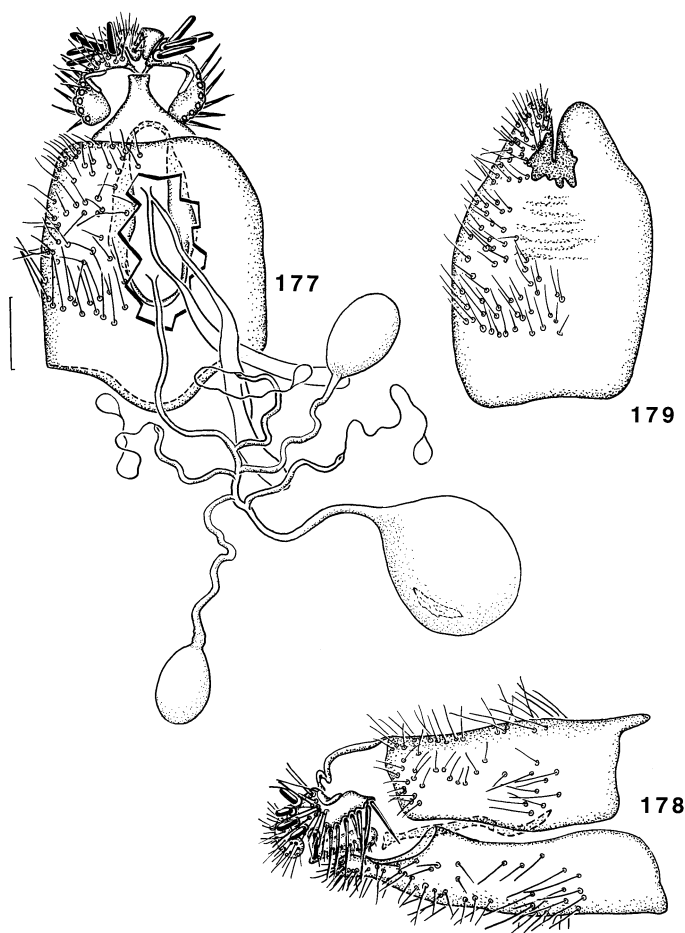
*Genitalia (Figs 177–179).* Furca closed; spermathecal sac trilobate, sacs globose, sac ducts and spermathecal ducts arranged as in Fig. 177; accessory glands symmetrical, unmodified.

#### *Male*

Unknown.

#### *Comments*

The alternate spermathecal sac arrangement and postocular ridge setae colouration are autapomorphic for this species. The specific epithet is derived from the Latin *intermedius*: that is



**Figs 177–179.** *Nanexila intermedia* Winterton & Irwin, sp. nov., genitalia (♀): 177, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 178, same, lateral view; 179, sternite 8, ventral view. Scale line: 0.2 mm.

between; pertaining to the intermediate form of the spermathecal sac arrangement. *Nanexila intermedia* is known from a single specimen from Thredbo, New South Wales (Fig. 183).

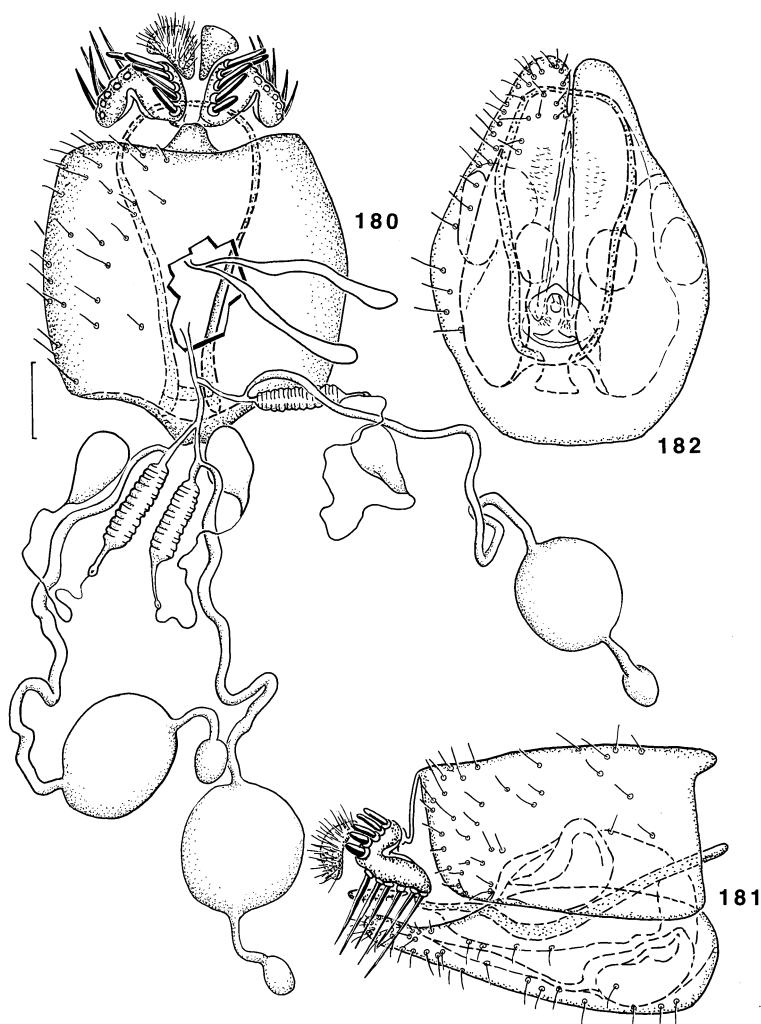
*Nanexila paradoxa* Winterton & Irwin, sp. nov.

(Figs 180–183)

*Material examined*

*Holotype*. ♀, Queensland: Scrub Rd, Brisbane Forest Pk, 27°25'05"S, 152°50'13"E, 15.xi.1997, S. Winterton, N. Power, D. White, malaise trap (QM). Condition: good.

*Paratypes*. **Queensland**: 2 ♀, 16 km up Davies Ck Rd via Mareeba, North Qld, 2.x.–5.xi.1984, Storey & Halfpapp (MEI#090743, 90744) (QDPI); ♀, Brookfield, Brisbane, 16.viii.1980, J. Conran (MEI#090745) (QDPI); 4 ♀, Scrub Rd, Brisbane Forest Pk, 27°25'05"S, 152°50'13"E, 25.xi.1997, S. Winterton, N. Power, D. White, malaise trap (UQIC).



**Figs 180–182.** *Nanexila paradoxa* Winterton & Irwin, sp. nov., genitalia (♀): 180, genitalia, dorsal view with tergite 8 part cut away to expose internal structures; 181, same, lateral view; 182, sternite 8, ventral view. Scale line: 0.2 mm.

*Diagnosis*

Scutum yellow to green-grey with faint irregular brown markings; wing with uniform pale infuscation; abdominal tergites with velutum on posterior margins; spermathecal sac arrangement trilobate, sacs with additional terminal constrictions to form distal lobe, spermathecal ducts joined in pairs to duct of each spermathecal sac lobe; sternite 8 with unusual convolute sclerotised structures internally.

*Description**Female*

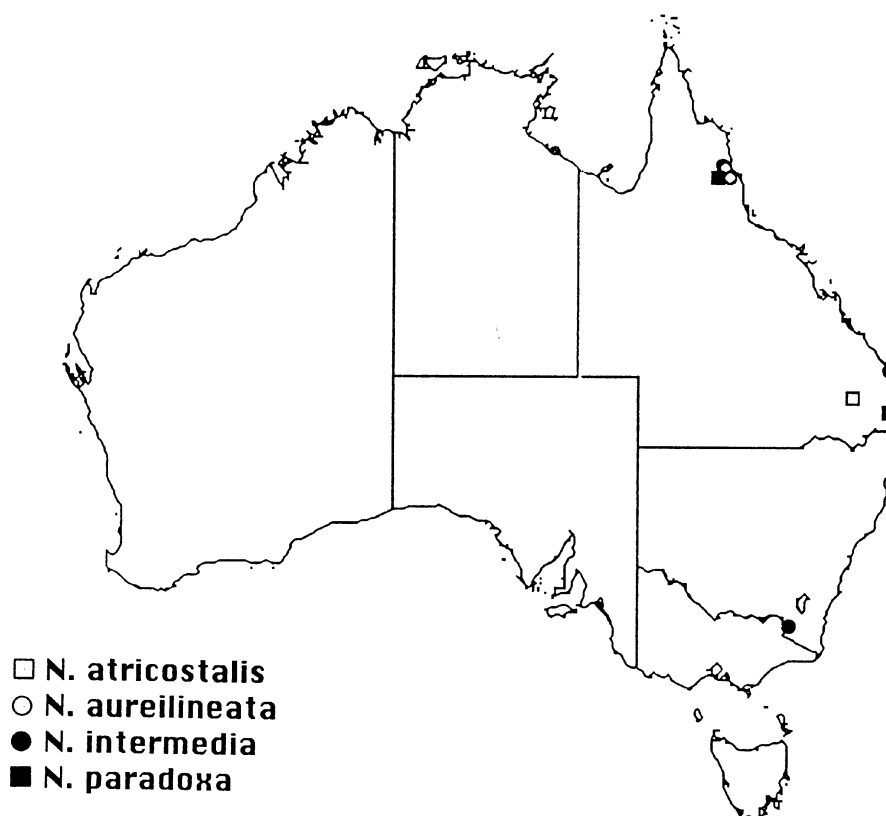
Body length: 8 mm.

*Head.* Frons brown, pruinose; eyes separate, distance approximately width of ocellar tubercle; occiput grey pruinose; postocular ridge with two rows of black setae.

*Thorax.* Scutum pale brown or grey, silver pruinose, patterned with brown; setae on pteropleural callus pale interspersed with two to three dark setae; coxae pale yellow, forecoxa sometimes dark; hind coxa with two lateral setae; legs pale. Scutal chaetotaxy: np 4; sa 2; pa 1; dc 3; sc 1.

*Abdomen.* Abdomen black, segments 3–7 pale yellow laterally, segments anteromedially with gold velutum, posterior and lateral margins with silver velutum; intersegmental membranes white; terminalia pale brown, tergite 8 black dorsally.

*Genitalia* (Figs 180–182). Furca long thin, closed; sternite 8 with convoluted sclerotised structures internally; spermathecal sacs trilobate, sacs globose, constricted distally to form a



**Fig. 183.** Distribution map for *Nanexila* species; *N. atricostalis* species-group: *N. atricostalis*, *N. aureilineata*, *N. intermedia*, *N. paradoxa*.



smaller lobe; spermathecae large, ovate; spermathecal ducts muscular, spermathecal ducts joined in pair to duct of each spermathecal sac lobe; accessory glands symmetrical, unmodified.

#### *Male*

Unknown

#### *Comments*

The unusual nature of the genitalia and reproductive system are autapomorphic for this species. The scutal chaetotaxy and trilobate spermathecal sac arrangement link this species closely with *N. atricostalis* and *N. aureilineata*. *Nanexila paradoxa* is recorded from two localities, one in far northern Queensland and the other in Brisbane (Fig. 183). The specific epithet is derived from the Latin *paradoxus*: strange, contrary to expectation; referring to the unusual shape of sternite 8.

### **Cladistic analysis of *Nanexila***

#### *Materials and methods*

##### *Data analysis*

Character polarity was determined using outgroup comparison (Nixon and Carpenter 1993). Those characters with more than one derived state were coded as either ordered or unordered. Cladistic analyses were performed using PAUP version 3.1.1 (Swofford 1993) and repeated using Hennig86 version 1.5 (Farris 1988). The matrix presented in Appendix 1 was prepared in MacClade version 3.01 (Maddison and Maddison 1992). Figure 184 was prepared using Clados version 1.2 (Nixon 1992) using delayed transformation (DELTRAN) optimisation. Branch support (Fig. 185) was calculated using Autodecay version 3 (Eriksson and Wikström 1996) and PAUP version 3.1.1.

##### *Outgroup selection*

The lack of any phylogenetic framework or internal hierarchy for Australian or world Therevidae made selecting an outgroup difficult. We believe the closest relatives of *Nanexila* occur in Australia, therefore selection of an outgroup required searching for a group from the described Australian genera. Since relationships of potential outgroups to the ingroup are unknown, several outgroups were chosen to represent the diversity within the family as best as possible. Outgroups chosen all belong to the *Agapophytus* group of genera, and included: *Acatopygia pulchella* Kröber, *Acupalpa pollinosa* Mann, *Agapophytus albobasalis* Mann, *Neodialineura striatithorax* Mann and *Squamopygia fascipennis* Kröber. We consider each species selected to be representative for their respective genera. The lack of precedent cladistic analyses on the greater Therevidae makes the definition of plesiomorphic and apomorphic character states rather subjective. Therefore, the scoring of character states in the cladistic analysis simply reflects the character polarity of the somewhat arbitrarily chosen outgroups to the ingroup. Only limited phylogenetic inferences are proposed here on the relationships of the outgroups. The character polarity of many characters used here may well be reversed in subsequent analyses on the family.

Based on external morphology and male genitalic characters, *Acupalpa* Kröber, *Agapophytus* and *S. fascipennis* Kröber represent a related sub-group of genera, while *Acatopygia* Kröber and *Neodialineura* represent another, possibly more ancestral, subgroup. This is reflected in the results of the cladistic analysis and suggests some basis for separation of *Agapophytus*, *Acupalpa*, *S. fascipennis* and related genera at the tribal level from the rest of the subfamily.

#### *Descriptions of characters and states*

Seventy-one characters comprising 167 states were used in the analysis. Most are binary, but characters 2, 4, 6, 13, 29, 43, 48, 50, 54, 59, 61 and 63 were coded as ordered, multistate characters each with three states, except 48 which had four states. Characters 1, 11, 23, 24, 36, 44, 56 and 67 were coded as unordered, multistate characters, each with three states except one and 23 which had four states, and 67 which had five states. Males of *N. lignyos*, *N. aureilineata*,

*N. intermedia* and *N. paradoxa*, and the female of *N. ligula* are unknown. Unknown character states were coded ‘?’. For brevity, outgroups are referred to hereafter by their generic names.

#### Head

1. *Body colour*: 0, yellow, brown; 1, wholly orange; 2, thorax orange-pink, abdomen yellow; 3, mostly black.
2. *Shape of flagellum*: 0, abruptly conical; 1, tapering; 2, long thin.
3. *Size of setae on scape and pedicel*: 0, most setae enlarged (Figs 14, 15); 1, only some enlarged (e.g. Figs 2–11).
4. *Presence of setae on flagellum*: 0, flagellum without setae; 1, flagellum with setae on base only (Fig. 16); 2, setae over entire length.
5. *Size of scape in plan view*: 0, wider than flagellum; 1, narrower.
6. *Size of antennal tubercle*: 0, greatly enlarged; 1, enlarged; 2, reduced.
7. *Length of flagellum*: 0, shorter than scape; 1, longer than scape.
8. *Head shape*: 0, pyriform; 1, round.
9. *Orientation of mouthparts*: 0, anteriorly; 1, ventrally.
10. *Transverse furrow on eye*: 0, present; 1, absent.
11. *Distance between eyes in male*: 0, eyes less than width of anterior ocellus apart; 1, eyes contiguous; 2, eyes greater than width of anterior ocellus apart.
12. *Number of rows of setae on postocular ridge of female*: 0, multiple rows of setae; 1, single row.
13. *Setae on the frons of male*: 0, long; 1, short; 2, absent.

#### Thorax

14. *Irregular patterning on scutum*: 0, present; 1, absent.
15. *Scutum with stripes*: 0, present; 1, absent.
16. *Colour of bases of minor setae on scutum*: 0, scutum pale with dark bases (Fig. 26); 1, scutum otherwise with pale bases.
17. *Scutum with quadrate*: 0, absent; 1, present (Figs 23, 24, 27).
18. *Size of minor setae on scutum*: 0, many or all enlarged; 1, small.
19. *Colour of notopleural setae*: 0, dark; 1, pale.
20. *Number of pairs notopleural setae*: 0, three (e.g. Fig. 22); 1, four (e.g. Fig. 23).
21. *Number of pairs of supra-alar setae*: 0, one (e.g. Fig. 22); 1, two (e.g. Fig. 23).
22. *Number of dorsocentral setae*: 0, greater than or equal to three; 1, less than three.
23. *Number of setae on coxa 1*: 0, three; 1, two; 2, four; 3, greater than four.
24. *Number of setal pairs on coxa 3*: 0, one; 1, two; 2, none.
25. *Colour of coxal setae*: 0, dark; 1, pale.
26. *Colour of setae on pteropleural callus*: 0, predominantly dark; 1, predominantly pale.
27. *Presence of additional hairs on coxae*: 0, numerous hairs; 1, hairs few or absent.
28. *Foretarsi*: 0, coloured; 1, not so.
29. *Hind femur setae*: 0, absent; 1, one; 2, multiple.
30. *Fore and hind femora with velutum mat on posteroventral surface*: 0, absent; 1, present.
31. *Wing*: 0, infusate (Figs 20, 21); 1, hyaline.
32. *Wing with cell m<sub>3</sub>*: 0, open; 1, closed.

#### Abdomen

33. *Male abdominal vestiture*: 0, without velutum; 1, with velutum.
34. *Female abdominal vestiture*: 0, without velutum; 1, with velutum.
35. *Abdomen markings*: 0, present; 1, absent.
36. *Setae on female abdominal tergite 2*: 0, modified (Fig. 17c,d); 1, unmodified; 2, absent.

#### Male genitalia

37. *Tergite 8 shape*: 0, medially emarginate (e.g. Fig. 130); 1, not emarginate (e.g. Fig. 31, 93).
38. *Lateral margins of tergite 8*: 0, long (e.g. Fig. 93); 1, short (e.g. Fig. 114).
39. *Epandrium dimensions*: 0, broad, width equal to length (e.g. Fig. 147); 1, elongate (e.g. Fig. 56).

40. *Epandrium with posterolateral processes*: 0, absent; 1, present (e.g. Fig. 56).
41. *Shape of epandrium anterior margin*: 0, emarginate (e.g. Fig. 39); 1, straight (e.g. 119).
42. *Epandrium shape*: 0, narrowed posteriorly (e.g. Fig. 56); 1, sides equidistant over entire length (e.g. Fig. 147).
43. *Size of setae on epandrium*: 0, uniformly enlarged; 1, various sizes (e.g. Figs 119); 2, uniformly reduced (e.g. Fig. 64).
44. *Size and arrangement of setae on gonocoxites*: 0, enlarged and randomly arranged; 1, enlarged and in series (e.g. Fig. 106); 2, mostly reduced and random (e.g. Fig. 69).
45. *Hypandrium and gonocoxites*: 0, separate (e.g. Fig. 59); 1, fused (e.g. Fig. 77).
46. *Gonocoxites*: 0, separate medially (e.g. Fig. 43); 1, fused medially (e.g. Fig. 77).
47. *Size of gonocoxal apodemes*: 0, reduced; 1, enlarged (e.g. Fig. 105).
48. *Outer gonocoxal process*: 0, absent; 1, present but reduced; 2, present; 3, with additional, ventral lobe (Figs 123, 124).
49. *Gonocoxites with patch of short, pale, pile ventrally*: 0, absent; 1, present.
50. *Ventral lobe*: 0, absent; 1, present; 2, enlarged.
51. *Ventral lobe with apical setae*: 0, absent; 1, present (e.g. Fig. 59).
52. *Gonostyli*: 0, weakly sclerotised apically; 1, heavily sclerotised apically.
53. *Inner gonocoxal processes*: 0, spatulate (e.g. Fig. 117); 1, narrow (e.g. Fig. 34).
54. *Apical setae on inner gonocoxal processes*: 0, enlarged; 1, reduced (e.g. Fig. 34); 2, absent (e.g. Fig. 105).
55. *Gonocoxal setae*: 0, dark; 1, some or all pale.
56. *Distiphallus*: 0, straight (e.g. Fig. 58); 1, curved ventrally (e.g. Fig. 104); 2, curved dorsally (e.g. Fig. 76).
57. *Distiphallus width*: 0, broad; 1, narrow.
58. *Distiphallus length*: 0, short (e.g. Fig. 50); 1, long (e.g. Fig. 122).
59. *Width of base of ejaculatory apodeme*: 0, less than 1/4 of the total length of the ejaculatory apodeme; 1, between 1/4 and 1/2 the length (e.g. Fig. 94); 2, greater than 1/2 the length (e.g. Fig. 140).
60. *Anterior end of ejaculatory apodeme*: 0, reduced; 1, enlarged.
61. *Ventral apodeme of aedeagus*: 0, not extending anteriorly past dorsal apodeme; 1, extending just past dorsal apodeme; 2, extending well past dorsal apodeme.
62. *Arms of ventral apodeme*: 0, not 'paddle' shaped; 1, 'paddle' shaped (Figs 75, 94, 157).
63. *Dorsal apodeme*: 0, simple, reduced; 1, broad, triangular; 2, forked.

#### *Female genitalia*

64. *Furca*: 0, closed (e.g. Fig. 53); 1, open (e.g. Fig. 36).
65. *Furca*: 0, weakly sclerotised; 1, sclerotised.
66. *Sternite 8*: 0, slightly cleft posteriorly (e.g. Fig. 38); 1, deeply cleft (e.g. Fig. 55).
67. *Spermathecal sac and spermathecal duct arrangement*: 0, simple, basal ducts (e.g. Fig. 61); 1, trilobate, basal ducts (Figs 53, 79, 161); 2, trilobate, alternate ducts (Fig. 177); 3, trilobate, paired ducts (Figs 125, 171, 174, 180); 4, simple with elongate parallel lobes, basal ducts.
68. *Spermathecal sac(s)*: 0, ovate (e.g. Fig. 45, 107, 171); 1, elongate (e.g. Fig. 61, 88, 125).
69. *Spermathecal sac(s)*: 0, small (e.g. Fig. 70); 1, large (e.g. Fig. 88).
70. *Duct of spermathecal sac(s)*: 0, short (e.g. Figs 88, 98); 1, long (e.g. Figs 79, 107).
71. *Base of sternite 8 cleft*: 0, unsclerotised; 1, sclerotised.

#### *Cladistic results and discussion*

Analysis of the data matrix in Appendix 1 by PAUP using 10 random addition sequences produced a single, most parsimonious tree of length 245 steps (Fig. 184). The analysis was repeated using Hennig86 with identical results. Tree characteristics include a consistency index (CI) of 0.39 and retention index (RI) of 0.63. There are a large number of convergences and reversals in the cladogram, particularly between the more terminal clades. Consistency index is interpreted as a measure of homoplasy, hence a measure of the 'goodness of fit' of the data to the cladogram (Kluge and Farris 1969; Sanderson and Donoghue 1989). Sanderson and

Donoghue (1989) found that the consistency index is negatively correlated with the number of taxa included in the analysis. The level of homoplasy found in this analysis is similar to other studies including this number of taxa (Sanderson and Donoghue 1989). The retention index is relatively high, indicating that a reasonable proportion of the synapomorphies in the matrix are present as homologies on the cladogram. To remove bias created by ordered character states, the analysis of the matrix was repeated with all multistate characters unordered. This gave an identical tree with a length of 240 steps, CI = 0.4 and RI = 0.64, indicating that ordering of multistate characters did not affect tree architecture.

*Neodialineura* is separated basally from the rest of the tree by the numerous characters including: absence of an outer gonocoxal process (character 48); ventral lobe absent (50) and distiphallus broad (57) (also present in *Agapophytus*).

*Acatopygia* is separated from *Acupalpa* clade + *Nanexila* by multiple setae on hind femur (character 29) and the ventral apodeme of aedeagus enlarged, extending anteriorly well past dorsal apodeme (72).

Synapomorphies for *Acupalpa* clade + *Nanexila* (clade 2) include: flagellum lengthened so that it is tapered (state 1) in *Nanexila*, to long and thin (state 2) in the *Acupalpa* clade (character 2); scape narrow in dorsal view (5); antennal tubercle reduced (state 1) in the *Acupalpa* clade and totally absent (state 2) in *Nanexila* (6); eye without transverse furrow (10); dorsal apodeme triangular or forked (63); furca well sclerotised (65).

*Acupalpa* + *Agapophytus* + *Squamopygia* form a distinct clade (clade 3) separated from *Nanexila* by: a long thin flagellum (character 2); flagellum with setae over entire length (4); less than three dorsocentral setae (22); foretarsi brightly coloured (28); fore and hind femora with patch of matt pruinescence (30); gonocoxites with patch of short, pale-coloured, ventral pile (49) and gonocoxal setae pale (55). *Acupalpa* is basal to *Agapophytus* and *Squamopygia*.

*Nanexila* is a large heterogeneous group (clade 5), but is clearly separated from the outgroups by the following synapomorphies: flagellum tapering (character 2); reduced antennal tubercle (6); a single seta on the hind femur (29); some or all epandrium setae reduced in size (43); gonocoxal setae either enlarged and arranged in series or reduced and randomly arranged, never enlarged and randomly arranged (44); and outer gonocoxal processes present (48). All characters supporting nodes within *Nanexila* are also listed in the descriptive comments for each of the species-groups.

*Nanexila* is basally divided into two clades, *N. atricostalis* species-group (clade 6) and *N. manni* + *N. palassa* species-groups (clade 9). The *N. atricostalis* clade is composed of *N. atricostalis* + *N. aureilineata* + *N. paradoxa* + *N. intermedia*, and is distinguished by: scape and pedicel with most setae enlarged (character 3); greater than four setae on forecoxa (excluding *N. intermedia*) (23); female abdomen with velutum (34); spermathecal sac arrangement trilobate or alternate (also in *N. livea*) (67). The *N. manni* + *N. pallassa* species-groups clade is defined by the following synapomorphies: four or less setae on forecoxa (23); wing hyaline (except *N. lignyos*) (31); female abdomen without velutum (34).

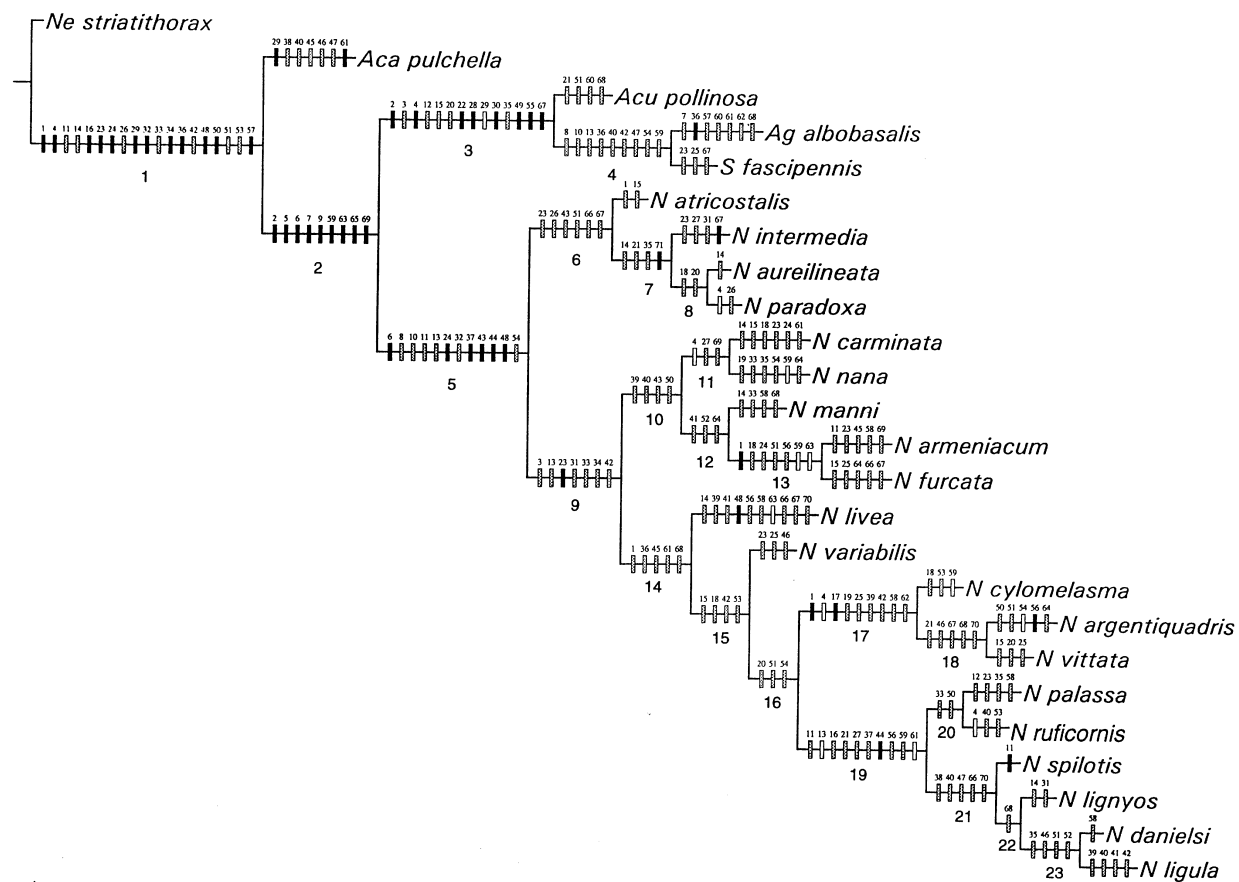
No clear synapomorphies separate the *N. manni* species-group (clade 10) from the rest of the *Nanexila* and is tentatively defined by the combination of characters listed in the descriptive taxonomy for the species-group. *Nanexila armeniacum* + *N. furcata* (clade 13) are clearly defined by completely orange body colouration (character 1).

The *N. pallassa* species-group clade (clade 14) is supported by the presence of: female with a modified patch of setae on abdominal tergite 2 (character 36) (also in *Neodialineura*); small medial and larger lateral setae on the epandrium (43); hypandrium fused with gonocoxites (45) (also in *N. armeniacum*).

*Nanexila argentiquadris* + *N. vittata* + *N. cylomelasma* (clade 17) form a clade distinct from the rest of the *N. palassa* species-group by: thorax orange-pink, abdomen yellow (character 1); scutum with quadrate between dc setae (17); pale np bristles (19); arms of ventral apodeme 'paddle' shaped (62).

Clade 19, comprising of *N. palassa* + *N. ruficornis* (clade 20), and the *N. danielsi* clade (clade 21), are well defined within the *Nanexila* by: scutum with bases of minor setae dark (character 16); tergite 8 medially emarginate (37); setae on gonocoxites enlarged with some arranged on series (44); base of ejaculatory apodeme greatly enlarged (state 2) (59).

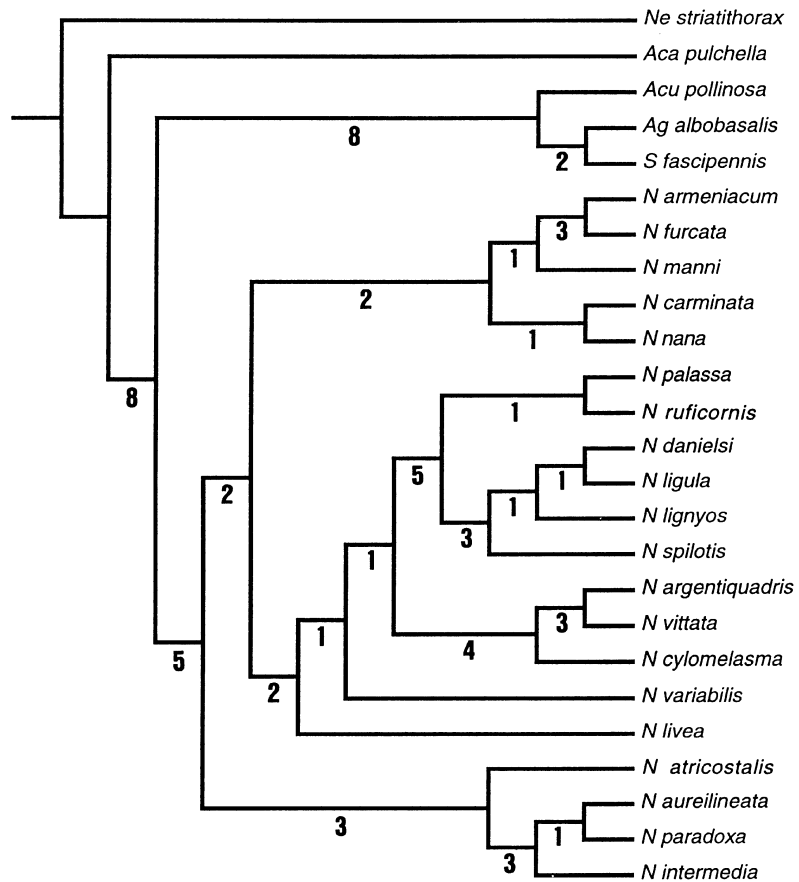
The *N. danielsi* clade (clade 21) is separated from *N. palassa* + *N. ruficornis* by: absence of



**Fig. 184.** Cladogram of relationships between species of *Nanexila* and the outgroups. Character numbers are presented above each hash. Dark hashes represent forward changes without homoplasy; grey hashes represent forward changes with homoplasy; pale hashes represent reversals. Branch numbers are presented beneath each node.

velutum on male abdomen (33); lateral margins of tergite 8 short (character 38); gonocoxal apodemes enlarged (47); ventral lobe reduced (50); sternite 8 deeply cleft posteromedially (66); duct of spermathecal sac long (70).

The cladistic analysis using PAUP and Hennig86 resulted in few synapomorphies for the basal nodes separating the species-groups within *Nanexila*. To test for the robustness of these basal clades, branch support was used. Branch support is defined as the extra tree length required for a branch to be lost in the strict consensus of near-most parsimonious trees (Bremer 1994). The greater the length of additional trees included in the consensus before a branch is lost, the greater the support for that branch by the data (Bremer 1994). Branch support is reported as a single unit for each additional step the length of the most parsimonious trees increase by, in which the branch is not lost. The higher the number, the more support for that particular branch on the most parsimonious tree. Bremer support of 0 for a node indicates that there is an equally most parsimonious tree with a different arrangement for that node. Branch support for each of the nodes on the cladogram is presented in Fig. 185. There is considerable support for nodes separating the basal outgroups *Neodialineura* and *Acatopygia* (clade 2) (8 steps) from *Acupalpa* clade + *Nanexila*. Support for *Nanexila* (clade 5) is much lower (3 steps), but still considerable. Within the *Nanexila* there is support for each of the species-groups (clades 6, 10 and 14 with 3, 2 and 2 steps respectively). Within the species-groups there was considerable support for the following clades: *N. armeniacum* + *N. furcata* (clade 13) (3 steps); *N. palassa* + *N. ruficornis* + *N. danielsi* + *N. ligula* + *N. lignyos* + *N. spilotis* (clade 16) (5 steps); *N. danielsi* + *N. ligula* + *N. lignyos* + *N. spilotis* (clade 19) (3 steps); *N. argentiquadris* + *N. vittata* + *N. cylomelasma* (clade 17) (4 steps); *N. argentiquadris* + *N. vittata* (clade 18) (3 steps).



**Fig. 185.** Cladogram of branch node support between clades of *Nanexila* species and outgroups. Numbers beside nodes represent the level of support for that branch on the most parsimonious trees.

Although different clades are clearly present, the major lineages of *Nanexila* are represented by few non-homoplasious synapomorphies. The large amount of heterogeneity in male and female genitalia suggests that the group may be subdivided at the generic level. Unfortunately the lack of well supported synapomorphies for the major groups makes their separation tenuous. Therefore, we do not consider their separation as distinct genera is warranted until the basal phylogeny of the genus can be better elucidated and the relationships of the genus to the greater therevid fauna can be established. The lack of males for *N. aureilineata*, *N. intermedia*, *N. paradoxa* and *N. lignyos* and the likelihood of collecting further undescribed taxa also precludes the erection of new, but poorly defined genera.

### Biogeography and temporal phenology of *Nanexila*

#### *Biogeography* (Figs 73, 91, 128, 164, 183)

Most of the species in the *Nanexila* group are known from relatively few specimens. Consequently the distribution patterns are likely to be an underestimate of their real range and can only be defined in relatively broad terms. The genus is almost undoubtedly endemic, with the known distributions of all *Nanexila* falling into roughly three major geographic regions: eastern Australia, western Australia and northern Australia. No species are recorded from Tasmania. The greatest diversity of species occurs in the south-western region with 10 species known, while the lowest diversity is in the northern region with only two species. Many species are restricted to a particular geographic region, although there is overlap between regions in species such as *N. manni* (Fig. 73), *N. danielsi* (Fig. 128) and *N. variabilis* (Fig. 164). Most species of *Nanexila* have a southern distribution, extending from south-western Western Australia around the southern margin of the continent to Victoria and northwards to south-eastern Queensland. Only *N. argentiquadris* and *N. cylomelasma* are atypical, with northern distribution patterns (Fig. 91).

#### *Temporal phenology* (Table 2)

Species of *Nanexila* from southern, western and eastern Australia are active during August through to April. Species from northern Australia (e.g. *N. argentiquadris*, *N. cylomelasma*) are

**Table 2.** Temporal phenology of *Nanexila*. Numbers represent collecting occasions regardless of the number of specimens captured

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
<i>N. armeniacum</i>											3	1
<i>N. carminata</i>				1								
<i>N. furcata</i>			1	1								
<i>N. manni</i>	9	2	4	1					3	3	15	19
<i>N. nana</i>										2		
<i>N. argentiquadris</i>				1				2		2		
<i>N. ruficornis</i>									1			
<i>N. cylomelasma</i>	1	1		1	1		1	2		1	2	
<i>N. danielsi</i>								1		5	4	
<i>N. lignyos</i>									1			
<i>N. ligula</i>								2			1	
<i>N. livea</i>	3	1	1						2	5	3	4
<i>N. palassa</i>									2	1		
<i>N. spilotis</i>								1		2	1	
<i>N. variabilis</i>			3							3	2	
<i>N. vittata</i>											4	
<i>N. atricostalis</i>				1					1			
<i>N. aureilineata</i>										2	1	1
<i>N. intermedia</i>	1											
<i>N. paradoxa</i>				1				2	1			

active for longer periods than southern species. The peak period for adult activity in most species is during the months of October and November.

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